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Response of greater sage-grouse to sagebrush reduction treatments in Wyoming big sagebrush

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Abstract

Vegetation treatments have been widely implemented in efforts to enhance conditions for wildlife populations. Yet the effectiveness of such efforts often lack rigorous evaluations to determine whether these practices are effective for targeted species. This is particularly important when manipulating wildlife habitats in ecosystems that are faced with multiple stressors. The sagebrush (*Artemisia* spp.) ecosystem has been altered extensively over the last century leading to declines of many associated species. Wyoming big sagebrush (*A. tridentata wyomingensis*) is the most widely distributed subspecies, providing important habitats for sagebrush-obligate and associated wildlife. Sagebrush often has been treated with chemicals, mechanical treatments, and prescribed burning to increase herbaceous forage species released from competition with sagebrush overstory. Despite many studies documenting negative effects of sagebrush control on greater sage-grouse (*Centrocercus urophasianus*) habitat, treatments are still proposed as a means of improving habitat for sage-grouse and other sagebrush-dependent species. Furthermore, most studies have focused on vegetation response and none have rigorously evaluated the direct influence of these treatments on sage-grouse. We initiated a 9-year (2011–2019) experimental study in central Wyoming, USA, to better understand how greater sage-grouse respond to sagebrush reduction treatments in Wyoming big sagebrush communities. We evaluated the influence of 2 common sagebrush treatments on greater sage-grouse demography and

*Retired

resource selection. We implemented mowing and tebuthiuron application in winter and spring 2014 and evaluated the pre- (2011–2013) and post-treatment (2014–2019) responses of sage-grouse relative to these management actions. We evaluated responses to treatments using demographic and behavioral data collected from 620 radio-marked female greater sage-grouse. Our specific objectives were to evaluate how treatments influenced 1) sage-grouse reproductive success and female survival; 2) sage-grouse nesting, brood-rearing, and female resource selection; 3) vegetation responses; and 4) forbs and invertebrates. Our results generally suggested neutral demographic responses and slight avoidance by greater sage-grouse in response to Wyoming big sagebrush treated by mowing and tebuthiuron. Neither mowing nor tebuthiuron treatments influenced nest survival, brood survival, or female survival. Selection for nest and brood-rearing sites did not differ before and after treatments. Females selected habitats near treatments before and after they were implemented; however, the strength of selection was lower after treatments compared with pre-treatment periods, which may be explained by a lack of response in vegetation and invertebrates following treatments. Perennial grass cover and height varied temporally yet did not vary systematically between treatment and control plots. Forb cover and species richness varied annually but not in relation to either treatment type. Perennial grass cover and height, forb cover, and forb species richness did not increase within mowed or tebuthiuron-treated areas that received 2 or 6 years of grazing rest compared with areas that received no grazing rest. Finally, forb and invertebrate dry mass did not differ between treated plots and control plots at mowing or tebuthiuron sites in any years following treatments. Results from our study add to a large body of evidence that sage-grouse using Wyoming big sagebrush vegetation communities do not respond positively to sagebrush manipulation treatments. Management practices that focus on the maintenance of large, undisturbed tracts of sagebrush will best facilitate the persistence of sage-grouse populations and other species reliant on the sagebrush steppe.

KEYWORDS

Artemisia tridentata, *Centrocercus urophasianus*, greater sage-grouse, invertebrate response, mechanical mowing, resource selection, sagebrush, survival, tebuthiuron, Wyoming

Respuesta del urogallo mayor a los tratamientos de control de la artemisa de Wyoming

Resumen

Los tratamientos para el control de vegetación han sido implementados ampliamente en un esfuerzo por mejorar las condiciones para las poblaciones de vida silvestre. Sin embargo, a menudo no hay evaluaciones rigurosas para determinar si estas prácticas son efectivas para las especies objetivo. Esto es particularmente importante cuando se manipulan hábitats de vida silvestre en ecosistemas que enfrentan múltiples factores de estrés. El ecosistema de artemisa (*Artemisia* spp.) ha sido muy alterado durante el último siglo, lo que ha provocado la disminución de muchas especies asociadas. La artemisa de Wyoming (*A. tridentata wyomingensis*) es la subespecie con distribución más amplia y proporciona hábitats importantes para especies de vida silvestre que usan o dependen de Artemisia spp. La artemisa a menudo es controlada con productos químicos, tratamientos mecánicos y quemas prescritas para aumentar las especies de forraje herbáceo y disminuir la competencia del dosel de artemisa. A pesar de que existen muchos estudios que documentan los efectos negativos del control de la artemisa en el hábitat del urogallo mayor (*Centrocercus urophasianus*), todavía se proponen tratamientos de control como un medio para mejorar el hábitat del urogallo y otras especies dependientes de la artemisa. Adicionalmente, la mayoría de los estudios se han centrado en la respuesta de la vegetación y ninguno ha evaluado rigurosamente la influencia directa de estos tratamientos de control en el urogallo. Iniciamos un estudio experimental de 9 años (2011–2019) en el centro de Wyoming, EE. UU., para comprender mejor la respuesta de los los urogallos mayores a los tratamientos de control en las comunidades de artemisa de Wyoming. Evaluamos la influencia de 2 tratamientos comunes de control de artemisa en la demografía y selección de recursos de urogallos. Implementamos la siega y la aplicación del herbicida tebuthiuron en invierno y primavera del 2014 y evaluamos las respuestas previas (2011-2013) y posteriores al tratamiento de control (2014-2019) por parte del urogallo en relación con estas acciones de manejo. Evaluamos las respuestas a los tratamientos de control utilizando datos demográficos y de comportamiento de 630 hembras de urogallo marcadas con dispositivos para telemetría.

Nuestros objetivos específicos fueron evaluar cómo los tratamientos de control influyeron en 1) el éxito reproductivo del urogallo y la supervivencia de las hembras; 2) anidación de urogallos, crianza de crías y selección de recursos por parte de las hembras; 3) respuestas de la vegetación; y 4) hierbas e invertebrados. Nuestros resultados generalmente sugirieron respuestas demográficas neutrales y una ligera evitación por parte del urogallo en respuesta al tratamiento de control de artemisa tratada con siega y tebuthiuron. Ni la siega ni los tratamientos de control con tebuthiuron influyeron en el éxito del nido, el éxito de la cría o la supervivencia de las hembras. La selección de los sitios de nidificación y crianza no fueron diferentes antes y después de los tratamientos de control. Las hembras seleccionaron hábitats cercanos a los tratamientos de control antes y después de su implementación; sin embargo, el nivel de selección fue menor después de los tratamientos de control en comparación con los períodos previos al tratamiento de control, lo que puede explicarse por la falta de respuesta en la vegetación y los invertebrados después de los tratamientos de control. La cobertura y la altura de pastos perennes variaron temporalmente pero no variaron sistemáticamente entre las áreas experimentales y de control. La cobertura herbácea y la riqueza de especies variaron anualmente, pero no en relación con ningún tipo de tratamiento de control. La cobertura y la altura de pastos perennes, la cobertura de hierbas y la riqueza de especies de hierbas no aumentaron en las áreas segadas o tratadas con tebuthiuron que recibieron 2 o 6 años de descanso de pastoreo en comparación con las áreas que no recibieron descanso de pastoreo. Finalmente, la masa seca de hierbas e invertebrados no fue diferente entre las áreas experimentales y de control en las áreas segadas o que recibieron tebuthiuron en ningún año posterior a los tratamientos de control. Los resultados de nuestro estudio se suman a una gran cantidad de evidencia de que el urogallo que usa las grandes comunidades de artemisa de Wyoming no responde positivamente a los tratamientos de control de artemisa. Las prácticas de manejo que se enfocan en el mantenimiento de extensiones grandes e intactas de artemisa facilitarán mejor la persistencia de las poblaciones de urogallos y otras especies que dependen de la estepa de artemisa.

Contents

INTRODUCTION

Management interventions often are implemented to enhance particular habitat conditions for wildlife populations (e.g., Hancock et al. 2011, Bergman et al. 2014, Peters et al. 2015). Vegetation treatments have been employed widely in both aquatic (Gowan and Fausch 1996, Eggleston et al. 1998, Syms and Jones 2000, Sass et al. 2006) and terrestrial (Sullivan and Moses 1986, Lochmiller et al. 1991, Hagar et al. 2004, Greenberg and Waldrop 2008) systems. Mechanical thinning, for example, can create forest canopy openings in mature hardwood stands that allow shade-intolerant plant species the opportunity to colonize treated areas (Steventon et al. 1998). Certain species assemblages also may increase use of treated vegetation depending on successional stage (Reinkensmeyer et al. 2007). Treatments typically are aimed at improving habitat quality for specific species and seasonal periods. For example, elk (*Cervus canadensis*) selected dense forest stands that were treated mechanically or via prescribed burning in northeastern Oregon, USA (Long et al. 2008). Increased mule deer (*Odocoileus hemionus*) fawn survival resulted when habitat treatments reduced pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) encroachment into shrubland communities on winter ranges (Bergman et al. 2014). By contrast, prescribed burning increased forage availability but not individual fitness of the northern bobwhite (*Colinus virginianus*; Carter et al. 2002). Although vegetation treatments may alter plant structure and composition, the evaluation of habitat quality via assessment of survival and reproduction is critically important for management efficacy (Van Horne 1983, Boyce and McDonald 1999). Robust study designs and clearly defined indicators to evaluate the success of treatments can help determine whether management practices are effective for target species (Block et al. 2001, Prach et al. 2019). This is particularly important given potential legacy effects of management practices in ecosystems faced with multiple stressors.

The sagebrush (*Artemisia* spp.) ecosystem covers approximately 43 million ha 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, habitat loss from fire, invasive species, and anthropogenic activities including agriculture and energy development (Leu et al. 2008, Davies et al. 2011, Chambers et al. 2017) has drastically altered the extent and composition of sagebrush (Knick et al. 2003, Davies et al. 2011). The contraction and alteration of the sagebrush ecosystem has contributed to 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, Smith et al. 2016, Green et al. 2017). Moreover, fire suppression in portions of the sagebrush ecosystem has resulted in greater woody cover (Davies et al. 2011), leading management efforts to reduce cover of big sagebrush (*Artemisia tridentata*) and pinyon pine–juniper (*Juniperus* spp.) forests. Treatments often have been implemented in big sagebrush communities to increase herbaceous production for domestic livestock and wildlife (Davies et al. 2009, Beck et al. 2012, Fulbright et al. 2018). Specifically, treatments are intended to reduce sagebrush cover and increase herbaceous production (Perryman et al. 2002, Dahlgren et al. 2006, Davies et al. 2009), albeit with mixed results.

Sage-grouse have experienced considerable population declines (Garton et al. 2011, Coates et al. 2021) and range contraction (Schroeder et al. 2004) primarily due to habitat loss, degradation, and disturbance (Braun 1998, Connelly et al. 2004, Doherty et al. 2008, Gregory and Beck 2014). Accordingly, sage-grouse have been the focus of considerable conservation actions to ameliorate the negative consequences of past land use decisions. As a result of these efforts, the United States Fish and Wildlife Service (USFWS) determined in 2015 that sage-grouse were not warranted for protection under the Endangered Species Act of 1973 (USFWS 2015). A focal point of sage-grouse conservation in recent years has been mitigating the loss of or improving sagebrush vegetation communities. Wyoming's Core Area Policy, for example, was implemented to limit disturbance in areas of Wyoming, USA, with the highest densities of breeding sage-grouse (Doherty et al. 2011). Similar priority areas for sage-grouse conservation were delineated throughout their range (USFWS 2013). At finer spatial scales within focal areas, the reduction of sagebrush cover also has been implemented with the intent of improving foraging habitat quality for sage-grouse, particularly during the brood-rearing period (Davies et al. 2009, Beck et al. 2012).

The sage-grouse is a sagebrush-obligate species that relies on sagebrush year-round for cover and food (Connelly et al. 2004, Crawford et al. 2004). Sage-grouse diets consist primarily of sagebrush leaves from late fall through early spring (Wallestad and Eng 1975) and sagebrush is the primary shrub species used for nesting concealment (Wallestad and Pyrah 1974, Connelly et al. 1991, Sveum et al. 1998, Moynahan et al. 2007, Kolada et al. 2009). Invertebrates and forbs associated with sagebrush communities are critical food resources for juvenile and adult sage-grouse, particularly during the late spring and summer periods (Wallestad and Eng 1975, Johnson and Boyce 1990, Barnett and Crawford 1994). Greater invertebrate consumption has been correlated with increased chick growth and survival (Johnson and Boyce 1990). Chick dependence on invertebrate-derived protein declines with age when forbs become the major food source of 2–10-week-old chicks (Klebenow and Gray 1968). Chick growth rates also increase with rapid transitions to diets dominated by forbs during early life stages (Blomberg et al. 2013, Smith et al. 2019*c*). Forbs comprise an important dietary resource of pre-incubating females because they contain higher levels of crude protein, calcium, and phosphorous compared with sagebrush (Gregg et al. 2008). Treating big sagebrush would therefore be most beneficial to sage-grouse populations if treated habitats increased the availability of important food resources, while maintaining adequate cover for concealment.

Typical sagebrush reduction treatments implemented for sage-grouse have included prescribed burns, mechanical removal, and chemical applications (Beck et al. 2012, Dahlgren et al. 2015). By 1974, nearly 2 million ha of the sagebrush steppe on federally managed lands had received sagebrush treatment (Vale 1974). Traditional methods of sagebrush removal included applications of 2,4-dichlorophenoxyacetic acid (2,4-D) to kill broad-leafed plants (e.g., Mueggler and Blaisdell 1958). Treatments of 2,4-D reduce sagebrush and forb cover, and increase grass cover (Blaisdell and Mueggler 1956, Sturges 1986). Burned sagebrush communities tend to respond similarly to those treated with 2,4-D, such that burns generally increase herbaceous vegetation in mature stands of Wyoming big sagebrush (*A.t. wyomingensis*; Davies et al. 2007). However, fires in big sagebrush communities can completely remove sagebrush within burn perimeters (Harniss and Murray 1973, Wambolt and Payne 1986), with little to no regeneration 6–14 years after treatment (Harniss and Murry 1973, Wambolt and Payne 1986, Beck et al. 2009). Mountain big sagebrush (*A.t. vaseyana*) canopy cover may recover as quickly as 25 years after fire, whereas Wyoming big sagebrush may require 25–120 years for canopy cover to return to unburned conditions (Wambolt and Payne 1986; Baker 2006, 2011). Moreover, application of 2,4-D and prescribed burning have shown little benefit for sage-grouse. Sage-grouse use of 2,4-D-treated strips of sagebrush for nesting was uncommon when live sagebrush cover was ≤5% (Klebenow 1970). Wintering sage-grouse used 2,4-D-treated sites less than their availability (Beck 1977). Other studies also concluded that 2,4-D-treated sagebrush areas were not beneficial to sage-grouse populations (Peterson 1970, Wallestad 1975). Similarly, researchers reported undesirable effects on sage-grouse nesting and brood-rearing habitat in large burned areas (Beck et al. 2009, 2011) and decreased male lek attendance at communal breeding grounds, or leks, following large fires (Connelly et al. 2000*a*, Coates et al. 2016, Smith and Beck 2018).

Management practices have shifted recently towards the reduction, but not elimination, of sagebrush cover via chemical and mechanical treatments to release forbs and grasses from competition with more dominant sagebrush overstories. Reduction in sagebrush cover with tebuthiuron depends on the rate of application of the active ingredient (Olson and Whitson 2002). At low rates (0.1–1.1 kg active ingredient [ai]/ha), tebuthiuron does not eliminate all live sagebrush cover (Whitson and Alley 1984, Johnson et al. 1996, Olson and Whitson 2002) and the woody structure of dead shrubs tends to remain. Similarly, mechanical treatments are implemented to selectively remove the crown or kill some sagebrush to reduce shrub canopy cover and density to make resources available for herbaceous plants and young sagebrush plants. Forb abundance tends to increase in mountain big sagebrush following mechanical and chemical treatments, potentially explaining an increased use of treated areas by sage-grouse (Dahlgren et al. 2006, Davies et al. 2012*b*). Stringham (2010) did not detect a difference in sage-grouse pellet density between aerated and control sites 1 and 2 years after treatment in mountain big sagebrush but detected greater pellet densities in aerated sites that were supplemented with grass and forb seedings compared to untreated areas in northeastern Utah, USA. Furthermore, brood-rearing sage-grouse selected areas closer to mechanically thinned mountain big sagebrush (Baxter et al. 2017).

The more widely distributed Wyoming big sagebrush (Knick et al. 2003) typically responds differently to treatments than mountain big sagebrush. Specifically, forb abundance does not generally increase over the short-term following treatments in Wyoming big sagebrush (Davies et al. 2012*a*, Hess and Beck 2014, Smith et al. 2019*b*), and any increase in forb cover often does not persist (>5 years post treatment; Hess and Beck 2012, Riginos et al. 2019). In north-central Wyoming, mechanically treated Wyoming big sagebrush sites did not meet minimum guidelines (Connelly et al. 2000*b*) for nesting and early brood-rearing sage-grouse habitats as much as 9 years after mowing (Hess and Beck 2012). Despite a large body of evidence that treating Wyoming big sagebrush has little benefit for wildlife (Beck et al. 2012), natural resource agencies continue to implement sagebrush control. Moreover, although studies have assessed the effects of sagebrush treatments on sage-grouse habitat use and selection in mountain big sagebrush communities (Klebenow 1970, Dahlgren et al. 2006, Baxter et al. 2017), similar responses have not been evaluated in Wyoming big sagebrush communities.

A retrospective study that accounted for wildfire, climate, and anthropogenic factors in the Wyoming Basins of central and western Wyoming found that lek attendance by male sage-grouse was negatively associated with prescribed burning and mechanical treatments as much as 11 years after treatment (Smith and Beck 2018). Only chemical treatments positively covaried with lek attendance, but benefits were not apparent until 11 years after treatments occurred (Smith and Beck 2018). By contrast, the number of males occupying leks in Utah doubled following treatments in mountain big sagebrush that reduced sagebrush canopy cover (Dahlgren et al. 2015). The implementation of small treatments (generally <200 ha) in a mosaic may increase sage-grouse abundance, particularly in mountain big sagebrush; however, grouse declines were reported after treating approximately 15% of sagebrush cover, also suggesting a potential threshold for treatments (Dahlgren et al. 2015). Whereas these studies identified broad-scale trends in sage-grouse abundance relative to sagebrush treatments, fine-scale information on habitat selection and demography in habitats altered by mechanical and chemical treatments are lacking. Moreover, the population growth and abundance of wildlife species depend upon fitness parameters. The evaluation of survival and reproduction is therefore paramount for assessments of habitat quality (Van Horne 1983, Boyce and McDonald 1999) and the efficacy of management practices (Block et al. 2001, Johnson 2007). No studies to date, however, have evaluated the nest, brood, or female survival of sage-grouse in response to big sagebrush treatments.

Our objectives were to experimentally evaluate the response of sage-grouse to mowing and tebuthiuron treatments of Wyoming big sagebrush. Specifically, we sought to address how sagebrush treatments influenced 1) sage-grouse reproductive success and female survival; 2) resource selection of grouse during the nesting, brood-rearing, and adult female life stages; 3) vegetation responses; and 4) forb and invertebrate biomass.

STUDY AREA

Our study occurred from 2011–2019 near Jeffrey City, Wyoming (42.49′N, − 107.83′W) and encompassed 4,595 km^2 across Fremont and Natrona counties. We used a 99% kernel utilization distribution (Worton 1989) generated from breeding and summer season locations of female sage-grouse to delineate the overall study area boundary (Figure 1). The area occurred in Sage-Grouse Core Areas within the Wyoming portion of the Western Association of Fish and Wildlife Agencies Wyoming Basins Sage-Grouse Management Zone II (MZ II; Stiver et al. 2006). Compared to range-wide sage-grouse habitat, soil moisture and temperature indicators typifying our study area supported moderate resilience to disturbance and resistance to invasion of annual grasses (Chambers et al. 2016, 2017). Elevation ranged from 1,594 m to 2,534 m. The 30-year normal (1981–2010) average annual

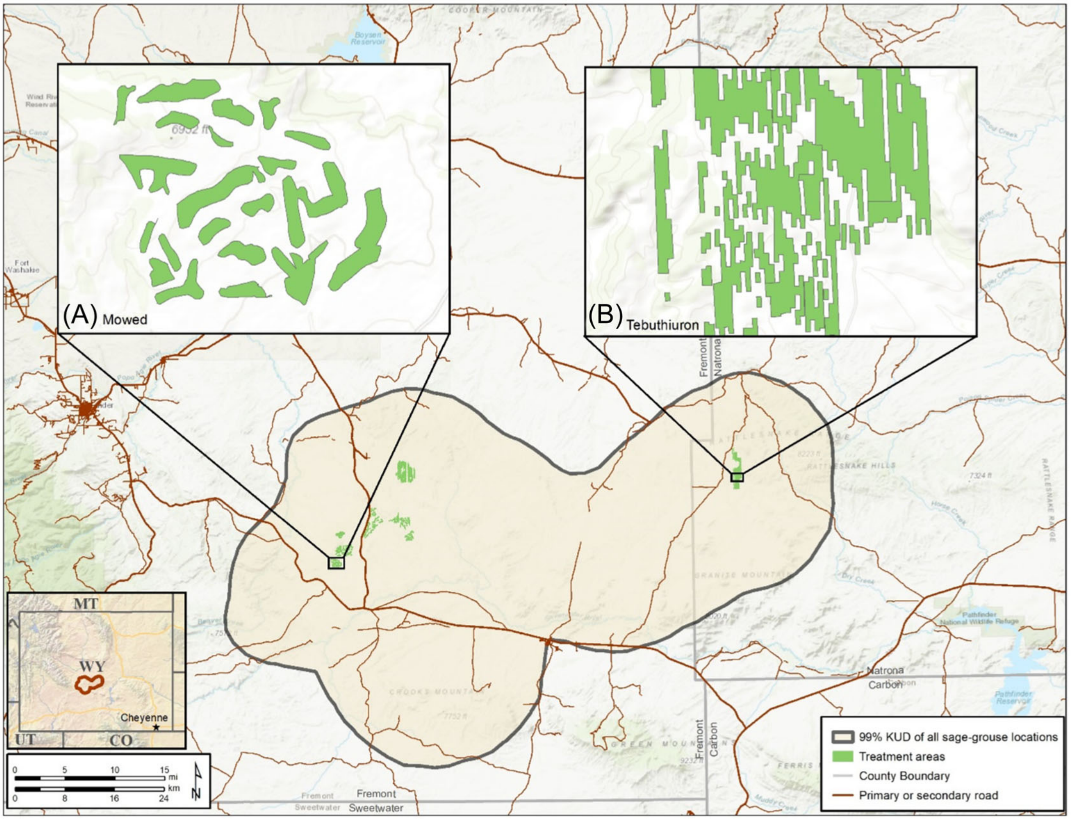

FIGURE 1 Study area defined by 99% kernel utilization distribution (KUD) of greater sage-grouse nesting, brood-rearing, and adult locations encompassing 4,595 km^2 in central Wyoming, USA, from 2011–2019. Two mowing (A) and 2 tebuthiuron (B) treatments were implemented in 2014 and occurred across 4.9 km^2 and 6.1 km^2 of the study area, respectively.

precipitation was approximately 27 cm (PRISM Climate Group 2012). Annual precipitation ranged from approximately 13.5 cm to 38.9 cm, with 2012 (13.5 cm) being the only study year with annual precipitation lower than the 30-year normal (PRISM Climate Group 2019). Average annual 30-year normal temperature was 6.1°C (PRISM Climate Group 2019). Approximately 78% of the lands in our study area were federally managed by the Bureau of Land Management (BLM), 14% were privately owned, and 8% were managed under state ownership. Wyoming big sagebrush was the dominant shrub in our study area. Mountain big sagebrush, basin big sagebrush (*A. t. tridentata*), black sagebrush (*A. nova*), rubber rabbitbrush (*Ericameria nauseosa*), and yellow rabbitbrush (*Chrysothamnus vicidiflorus*) were also common. Common perennial forbs included buckwheat (*Eriogonum* spp.), phlox (*Phlox* spp.), tailcup lupine (*Lupinus caudatus*), and yarrow (*Achillea millefolium*). Common grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread (*Hesperostipa comata*), and western wheatgrass (*Pascopyrum smithii*). Cheatgrass (*Bromus tectorum*) was largely absent in the area during the study (K. T. Smith and J. L. Beck, University of Wyoming, unpublished data). Common invertebrates included ants (Hymenoptera), beetles (Coleoptera), caterpillars (Lepidoptera), and grasshoppers (Orthoptera). The predominant land use across the study area was livestock grazing. We obtained information for allotments managed by the BLM in Wyoming from the Rangeland Administration System. Livestock stocking rates ranged from 2.5 ha/animal unit months in the Big Pasture allotment in the western portion of our study area to 6.9 ha/animal unit months in the Blackjack Ranch allotment in the eastern portion of our study area. The study area occurred in portions of 5

BLM Wild Horse Herd Management Areas. Uranium mining once occurred across portions of the study area and there were a few small producing oil and gas fields during our study.

METHODS

Study design

We experimentally manipulated habitat to evaluate the influence of mowing and tebuthiuron, 2 common sagebrush treatments, on the reproduction and survival of female sage-grouse from 2011–2019. We collected pre-treatment data on nest, brood, and adult female survival during spring and summer 2011–2013 across the entire study area. We used brood-rearing locations (first 2 weeks following nest hatch) collected during 2011 and 2012 to identify important brood-rearing habitat features. We developed a resource selection function (RSF) with remotely sensed predictors to create an RSF surface of relative probability of early brood-rearing resource 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 study areas (2 mowed, 2 tebuthiuron, and 2 off-site controls; see Appendix A for a detailed description). Specific usage of study sites (e.g., treated vs. off-site control) to address each objective are described in respective analyses below.

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 geographic information system predictor variables from models used to generate the RSF (Appendix A) to further delineate suitable treatment locations. In addition, we removed locations available for treatment when shrub cover was <2 standard deviations of mean shrub cover at sage-grouse use locations (7.9%; Homer et al. 2012) to avoid treating areas containing sparse shrub cover, removed locations <100 m from water, and removed areas with >15% slope.

We conducted mowing and tebuthiuron treatments during winter and spring 2014. Mowing occurred across 2.2 km^2 and 2.7 km^2 of the 2 mowing study sites, within which we reduced shrub height to approximately 25.4 cm. We aerially broadcasted tebuthiuron treatments (Spike® 20 P, Dow AgroSciences, Indianapolis, IN, USA; applied at 0.22 kg/ha active ingredient by Ag Flyers, Inc., Torrington, WY, USA) during 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 at tebuthiuron study sites, respectively. Live Wyoming big sagebrush percent canopy cover was reduced by approximately 52.9% in mowed (treated: 8.4 ± 1.0% [SE]; untreated control: 17.9 ± 0.9%) and 46.2% in tebuthiuron-treated (treated: 15.6 ± 2.6%; untreated control: 29.0 ± 2.8%) areas, compared with paired untreated areas during 2017 (K. T. Smith, unpublished data). We applied treatments in a mosaic pattern (Figure 2), and individual treatment polygons averaged 3.3 ± 0.19 ha in mowed and 4.2 ± 0.8 ha in tebuthiuron-treated sites. Treatments followed Wyoming Game and Fish Department (WGFD) protocols (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 untreated sagebrush (Dahlgren et al. 2006).

The only exception to the WGFD (2011) protocol was that instead of grazing rest for 2 growing seasons after treatments, we installed exclosures to measure post-treatment vegetative response in the absence of grazing. This was necessitated by the fact that only 1 allotment in the 6 study areas had cross-fencing and a rotational grazing system. The remaining study areas occurred in areas with season-long continuous grazing, making evaluations of ungrazed post-treatment vegetation response impossible without exclosures. Therefore, in May 2014 a contractor installed 6 30-m × 60-m exclosures in each mowing study site and 6 30-m × 80-m exclosures in each tebuthiuron-treated site to control for livestock grazing. Exclosures constructed in herbicide-treated areas were larger to account for potential herbicide leaching into the untreated side. The general design of exclosures was to exclude a

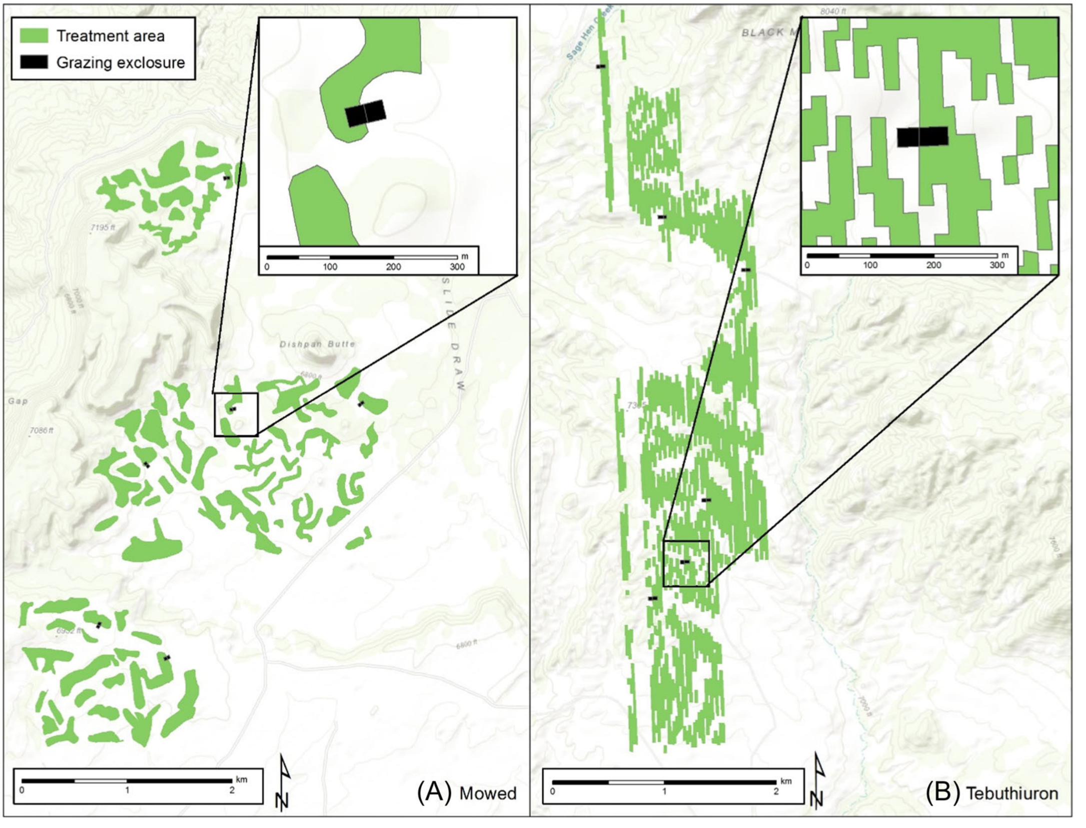

FIGURE 2 Configuration of mowing (A) and tebuthiuron (B) treatments (shaded polygons) implemented in 2014 to evaluate greater sage-grouse responses and surrounded by non-treated Wyoming big sagebrush (white) in Fremont and Natrona counties, central Wyoming, USA.

30-m × 30-m area of untreated sagebrush with an adjoining 30-m × 30-m area excluding livestock grazing in treated sagebrush. The contractor removed 3 exclosures (temporary exclosures) in each of the 4 treatment study areas in April 2016 so we could evaluate vegetation response after 2 years of grazing rest.

Animal capture and monitoring

We captured female sage-grouse with hoop nets and spotlights (Giesen et al. 1982, Wakkinen et al. 1992) during spring and summer each year. In March and April, we focused capture efforts near leks. Because sage-grouse often congregate in late summer (Dalke et al. 1963), we used nighttime roost locations of radio-marked females to capture additional females in late July and August each year. We aged (yearling or adult) captured females based on the shape and condition of the outermost wing primaries (Braun and Schroeder 2015). We affixed either 22-g polyvinyl chloride (PVC)-covered wire-necklace very high frequency (VHF) transmitters (Model A4060 or G10 UltraLITE GPS Logger Advanced Telemetry Systems Incorporated, Isanti, MN, USA), or rump-mounted Global Positioning System (GPS) transmitters (22-g PTT-100 Solar Argos/GPS PTT, Microwave Telemetry, Columbia, MD, USA). The GPS transmitters were programmed to collect 5 locations per day from 15 March to 30 April (at 0700, 1000, 1300, 1600, and 2400) and 6 locations per day from 1 May to 24 August (at 0600, 0900, 1200, 1500, 1800, and 2400) with the Argos system (CLS America, Largo, MD, USA). We rarified locations collected from GPS-marked females by randomly selecting 1 midday (i.e., 0900, 1200, 1500) location for each individual per week to be consistent with tracking intervals of VHF-marked females. Marked females were located approximately once per week from late April through mid-August each year with R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA, USA). We employed a fixed-wing aircraft to locate individuals that we were unable to locate with ground-based telemetry.

We located nests of VHF radio-marked females by homing in on the transmitter'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 of GPS-marked individuals after females left the location to verify nests and determine nest fate. We defined nest success when ≥1 egg hatched (Rotella et al. 2004). When a female successfully hatched a nest, we determined brood fate by visually observing the female with ≥1 chick or the female exhibited brooding behavior (e.g., distraction display, feigning injury) during telemetry visits (Kirol et al. 2012). If determined the brood had failed, we assigned the date of brood loss as the midpoint between successive visits when the female had and did not have chicks. We confirmed brood status with night-time spotlight counts at approximately 35 days post hatch (Walker 2008, Kirol et al. 2015). We considered a female to have successfully reared a brood when ≥1 chick was present with the female during night-time counts. We assessed brood survival and resource selection (described below) over the same 35-day post-hatch period. We continually monitored females irrespective of nest or brood fate throughout the study period to assess female survival.

Vegetation sampling

In each of the 4 treatment study areas, we sampled 10 treated locations, 10 untreated control locations adjacent to treated areas, and 6 exclosures (permanent and temporary) during each year following treatments (2014–2019). The mean distance from untreated control locations to a treatment was 122 m (range = 42–278 m) to ensure similar habitat physiognomy and climatic conditions. Sampling dates of all locations corresponded to the early brood-rearing period during each year (late-May to late-June), and we began sampling within 1 week following the first successfully hatched nest.

We evaluated vegetation and ground cover microhabitat parameters at each location along 2 perpendicular 30-m transects centered at each location and oriented in cardinal directions (Appendix B). We measured vegetation to be consistent with sampling that occurred at sage-grouse use locations in our study (Smith et al. 2018*a*, 2019*c*). We estimated herbaceous and ground cover attributes using the Daubenmire (1959) technique in 20-cm × 50-cm quadrats (*n* = 17 quadrats per location) placed at the center of each plot and at 1.0 m, 3.0 m, 7.5 m, and 12.5 m from the plot center in each cardinal direction. We recorded shrub canopy cover with the line intercept method and computed percent cover for each shrub species (Canfield 1941, Wambolt et al. 2006). We recorded shrub density by counting shrubs rooted within 1-m belt transects positioned along the right side of each 30-m transect. We measured visual obstruction using a Robel pole (dm; Robel et al. 1970) placed in the center of each location with measurements recorded from a distance of 5 m, 10 m, and 15 m at 1-m height from each cardinal direction. We measured the droop height of perennial and residual perennial grasses in each 20-cm × 50-cm quadrat and the height of each shrub encountered along each 30-m line transect.

Forb and invertebrate sampling

We simultaneously sampled food forb (see Kirol et al. 2012 for list of food forbs) and invertebrates at the 10 treated and 10 untreated control locations within each of the 4 treatment study areas following treatment from

2014–2018. Methods followed a previous evaluation of forb and invertebrates at treatment and sage-grouse brood-rearing locations in our study system (Smith et al. 2019*b*). We sampled forbs and invertebrates at the same 30-m transects used for vegetation sampling. We placed circular quadrats (1-m^2) randomly at either 3 m, 6 m, 9 m, or 12 m without replacement from the center of each plot. We fit quadrats used to sample invertebrates with mesh window screening to prevent escape. We used an invertebrate vacuum with a 2-minute duration per quadrat (Model 1612, The John W. Hock Company, Gainesville, FL, USA; Schreiber et al. 2015). We clipped annual and perennial food forbs in an adjacent 1-m^2 quadrat. We stored invertebrate samples in a freezer before processing. We dried forbs (g) and invertebrates (mg) in a forced-air drying oven at 60°C for 48 hours to obtain dry matter (g DM/4 m^2) at each sampling site.

Survival analyses

Statistical analyses

We evaluated nest survival, brood survival, and female survival using mixed Cox proportional hazards models (Cox 1972). For each vital rate, we ran 2 separate sets of models to individually evaluate potential effects of mowing and tebuthiuron treatments. We assessed nest success using time-to-event models over a 27-day incubation period. We used a 27-day incubation period because on average, successful nests from GPS-equipped females ($n = 30$) incubated for 27 days. We used the interval counting process to assess weekly brood and female survival (Anderson and Gill 1982), wherein we assessed brood survival from hatch to 5 weeks and adult female survival 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). We assigned dates of nest fates and brood and female mortalities to the mid-point date between monitoring intervals when nest fate, brood loss, or mortality of females occurred. We explored the possibility of transmitter types influencing demographic rates (Severson et al. 2019) and included transmitter type (VHF transmitter set to reference category) in all models if demographic rates differed. We also, included female age in all models if demographic rates differed by age.

Predictor variables

We constructed environmental models for each demographic rate to account for potential variation in survival prior to evaluating the influence of sagebrush treatments. The normalized difference vegetation index (NDVI) estimates net plant primary production (Pettorelli et al. 2011) and has been positively correlated with sage-grouse resource selection, population growth, and recruitment (Blomberg et al. 2012, Dinkins et al. 2014). Precipitation positively influences sage-grouse population growth and individual vital rates (Blomberg et al. 2012, Guttery et al. 2013), though the timing of precipitation is a salient consideration for nest and chick survival (Hannon and Martin 2006, Moynahan et al. 2007). For these reasons, we included estimates of remotely sensed big sagebrush percent canopy cover (Homer et al. 2012), NDVI (250-m resolution; Vermote 2021), and precipitation (nest and brood models only; PRISM Climate Group 2019) for consideration in base environmental models. The NDVI estimates were available every 8 days, so we matched the nearest NDVI value to the date of estimated nest initiation, or location date for brood and female locations. We summed precipitation data over 1, 3, and 5 days before estimated nest fate and before each brood location was recorded. Sage-grouse nest survival may be lower 1 day after significant precipitation events (Moynahan et al. 2007, Webb et al. 2012). We therefore expected that precipitation could negatively influence nest fate or brood survival over a short time interval. We did not expect a similar relationship with female survival, however, so we did not include precipitation in adult survival models. Nonetheless, annual precipitation has been related to recruitment and survival in sage-grouse populations (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 classified nests based on their spatial association with treatments. We used all locations collected from females equipped with GPS transmitters that initiated a nest to determine the distance between their nest location and all other locations used over the 3-week period before nest initiation, as this is the period when females mate and begin seeking nest locations (Schroeder et al. 1999). We then calculated the maximum distance from any location to the nest location for each GPS-marked female over the period preceding nest initiation and used the median value as the radius for a circular analysis region around nests from all marked females (median = 3.47 km, from n = 47 individual-years). We categorized nests as treatment nests when they were within 3.47 km of a treatment or the future location of a treatment. Our definition of treatment nests assumed that habitats within 3.47 km of a nest were available to the incubating female during the period leading up to nest initiation. Nests within a treatment site but having a circular analysis region that did not overlap with a treated area were considered untreated control nests. We compared treatment and untreated control nests to those from individuals in off-site control areas. The median distance of nests located in off-site control study sites to any treatment was 20.7 km (range = 10.3–28.1 km). We used nests in off-site control study sites for comparison in both mowing and tebuthiuron models. Nest assignment (treatment, untreated control, and off-site control) was a categorical predictor, wherein we set treatment nests as the reference category for comparison in all models. We included only first nests in analyses because renesting events generally are less common and often experience increased survival compared to first nest attempts (Taylor et al. 2012). For brood and female survival models, classifying individuals as either treatment or untreated control was confounded by potential carry-over effects as individuals could move between locations. Rather than assigning categorical treatment predictors, we therefore assessed the influence of treatments based on the distance of a brood or female to the nearest treatment during each relocation event.

To evaluate the influence of treatments on individual demographic rates, we followed a sequential modeling approach (Arnold 2010). We used study site and year as random factors for nest survival models. For brood and adult models, we included individual and year as random factors. We ran univariate models to select a single precipitation variable (nest and brood models) that was most supported based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c; 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. If environmental models showed improvement over null models, we included variables in the most supported models (base environmental model covariates) in addition to treatment covariates to assess the influence of treatments on sage-grouse demographic rates. Variables used to assess the influence of treatments included treatment type (in nest models) or distance to treatment (in brood and adult models), period (pre- or post-treatment), and a treatment × period interaction term. A significant interaction between treatment and time indicated a change in the measured demographic parameter before and after treatments were implemented. We considered support for a treatment × period interaction when modeled coefficients had 95% confidence intervals that did not overlap zero.

Resource selection analysis

Defining availability in treated study areas

We aimed to ensure that treated areas were available to individuals in resource selection modeling efforts. That is, assessing availability at the level of the entire study area was potentially misleading because treated areas were not available to every radio-marked individual in our study. Sage-grouse exhibit high fidelity to seasonal habitats (Berry and Eng 1985, Fischer et al. 1993, Holloran and Anderson 2005), and are unlikely to make large-scale within-season movements to novel areas once they have established a seasonal range. Therefore, we defined the extent of available habitat within each of the 4 treated study sites based on nesting locations in relation to treatment areas. We considered nests as treatment nests when they were within 3.47 km of a treatment (described in demographic analysis). We then assigned nests to the treatment type and study site with which they were spatially associated. We did not use locations from females that nested farther than 3.47 km from a treatment to delineate the extent of available habitat further. We pooled all summer locations of individuals that had treatment areas available to them during the nesting period and generated 90% kernel utilization distributions (KUDs; default bivariate; Worton 1989) to determine available habitat for each of the 4 treatment areas (Figure 3). We then included locations of nests, brood-rearing females, and females from all locations collected over the duration of the study that were inside each KUD in each of the treatment study sites. We assigned use locations to treatment study site and randomly generated available locations ($n = 25$ per use location) separately for nest, brood-rearing, and female locations within each treatment study site.

Predictor variables

We evaluated the influence of remotely sensed predictor variables at the raster cell scale (30 m; hereafter local scale) 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). We chose these analysis regions based on sage-grouse biology (Holloran and

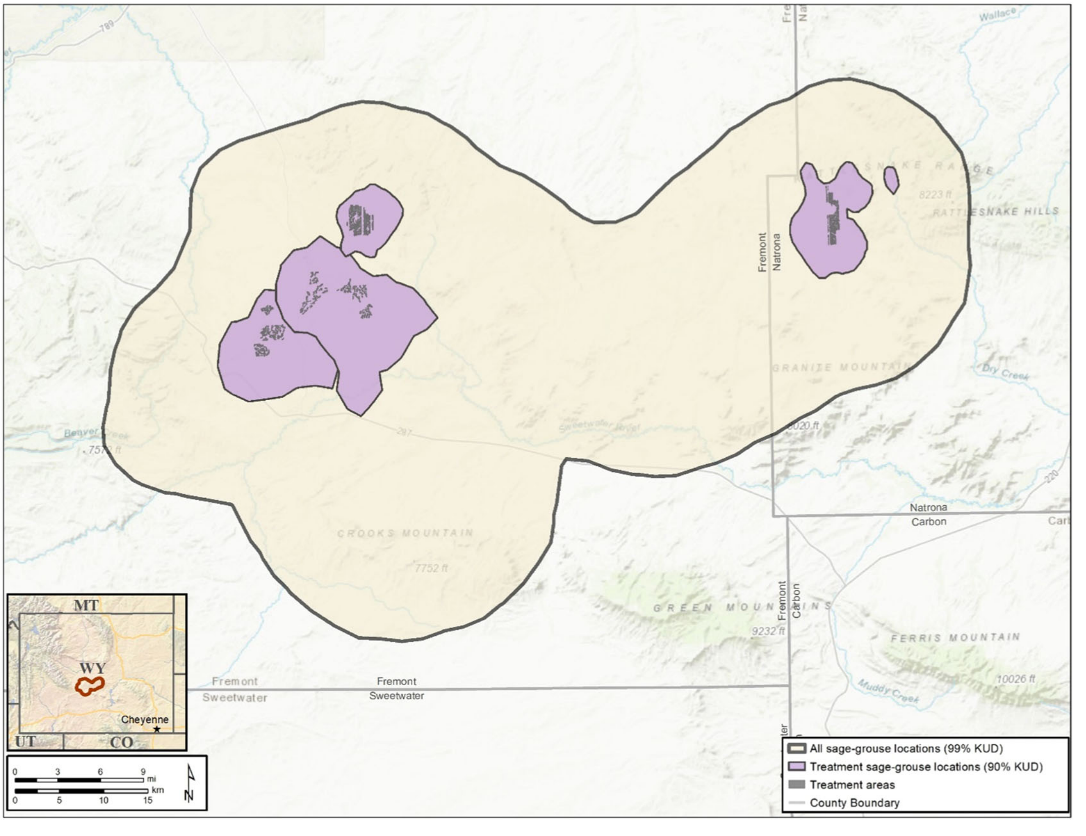

FIGURE 3 Available greater sage-grouse habitats within each of the 4 treatment areas delineated by 90% kernel utilization distributions (KUD) in Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

Anderson 2005, Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015) and federal management directives (BLM 2015). We used a 30-m digital elevation map (U.S. Geological Survey 2011) to calculate slope (%). We derived remotely sensed vegetation layers from the National Land Cover Database Shrubland Products (Xian et al. 2015). We considered big sagebrush cover (%), herbaceous cover (%), and shrub height (cm). We quantified surface disturbance (areas of bare ground resulting from removal of vegetation) with heads up digitizing following the Wyoming DDCT protocol (Wyoming Geographic Information Science Center 2016). Where possible, we time-stamped disturbances for each year to account for ongoing activities in some areas. We derived treatment variables from spatial data created by demarcating the perimeter of each treatment with a handheld GPS (Garmin GPSmap 62 s, Garmin, Olathe, KS, USA). The 5 treatment variables we assessed included Euclidean distance to treatment and the amount of treatment (ha) within each of the 4 analysis regions. We extracted values for each predictor variable at each used and available location.

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 female sage-grouse habitat selection. We subset data by treatment to generate separate models for each life stage (nesting, brood-rearing, female) and treatment type (mowing and tebuthiuron). All models contained the random effects of treatment study site and individual (nested within each year). We first evaluated the influence of all variables except those related to treatments for each model. We included female age (yearling or adult) in all models if resource selection differed by age.

This approach allowed us to develop a base model that accounted for environmental and anthropogenic features that may influence resource selection. For predictors that were assessed across multiple analysis regions, we determined the most predictive of each analysis region in a single-variable framework and retained the most supported variable based on AIC_c (Burnham and Anderson 2002). We explored all variable combinations with package MuMIn in R (Barton 2020). We did not allow correlated predictors ($|r| > 0.7$) in the same model. If more than 1 model was competitive (i.e., multiple models within 4 AIC_c), we considered the model with the fewest covariates as the base model. We compared the base model to 5 treatment models, which each contained a single treatment variable (described above), plus the treatment × period interaction term in addition to covariates from the base model. We selected the most supported treatment model based on the lowest AIC_c 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. We considered statistical significance when model coefficients had 95% confidence intervals that did not overlap zero.

Vegetation analysis

We used linear mixed models (package nlme; Pinheiro et al. 2016) to evaluate the response of vegetation to mowing and tebuthiuron treatments. Fixed factors included treatment type (treatment, untreated control) and year, with plot (year nested within plot) treated as a random effect. We constructed separate models for each treatment type (mowing or tebuthiuron) and vegetation response. We used least square means with Tukey adjustments to assess *post hoc* differences between treatment and untreated controls across sampling years when the main effects were significant (package lsmeans; Lenth 2016). The vegetation characteristics we evaluated included live big sagebrush cover (%), live big sagebrush height (cm), perennial grass cover (%), perennial grass height (cm), forb cover (%), and forb species richness. Statistical significance was set at alpha = 0.05.

We used additional linear mixed models and *post hoc* comparisons to evaluate vegetation at mowing and tebuthiuron treatments compared to treatments within temporary and permanent exclosures. Fixed factors included type (treatment outside exclosure, temporary exclosure, permanent exclosure) and year, with plot (year nested within plot) treated as a random effect. The vegetation characteristics we evaluated were perennial grass cover (%), perennial grass height (cm), forb cover (%), and forb species richness. Statistical significance was set at alpha = 0.05.

Forb and invertebrate analysis

We used linear mixed models (Pinheiro et al. 2016) to evaluate the response of forbs and invertebrate biomass measured as DM (DM; g DM/4 m^2 and mg DM/4 m^2, respectively) to mowing and tebuthiuron treatments, separately. Fixed factors included treatment type (treated or untreated control) and year (2014–2018), with plot treated as a random effect. We used least square means with Tukey adjustments to assess *post hoc* differences between treatment and controls across sampling years when the main effects were significant (package lsmeans; Lenth 2016). Statistical significance was set at alpha = 0.05.

RESULTS

Survival

From 2011–2019, we captured and radio-marked 620 female sage-grouse (mean = 69 individuals per year, range = 27–96). We obtained 716 nest (638 first attempts), 1,598 brood-rearing, and 7,493 female locations for analysis (Table 1). Neither nest nor brood survival differed between females affixed with GPS or VHF transmitters ($P \geq 0.14$). However, females equipped with GPS transmitters had lower survival compared to those equipped with VHF transmitters ($\beta = -1.02$, 95% CI = −1.46 to −0.59), so we included transmitter type in subsequent female survival models. Nest, brood, and female survival did not vary by age ($P \geq 0.10$). Overall nest survival rates, not incorporating the influence of treatment, were generally higher in years before treatments (2011–2013; 0.48, 95% CI = 0.41 to 0.56) compared with years after treatments (2014–2019; 0.39, 95% CI = 0.35 to 0.44). Overall brood survival to 35 days post hatch during pre-treatment years was higher (0.76, 95% CI = 0.67 to 0.87) than years following

TABLE 1 Number of nests, brood, and female greater sage-grouse locations used to evaluate the influence of mowing and tebuthiuron treatments on greater sage-grouse demographic rates, Fremont and Natrona counties, central Wyoming, USA, 2011–2019. Numbers in parenthesis indicate the number of females associated with nest, brood, and female locations.

	Pre-treatment (2010–2013)			Post-treatment (2014–2019)		
	Mow	Tebuthiuron	Off-site control[a]	Mow	Tebuthiuron	Off-site control[a]
Nests	61[b] (51)	46[b] (40)	52 (43)	164[b] (123)	176[b] (120)	139 (93)
Broods	245 (35)	195 (27)		656 (100)	502 (77)	
Female	1,381 (168)	763 (99)		2,856 (265)	2,493 (228)	

[a]Used in nest survival models. Off-site control nests were from individuals captured in the 2 untreated study areas. The median distance of nests located in off-site control study sites to any treatment was 20.7 km (range = 10.3–28.1 km).

[b]Included 16 and 40 nests considered untreated controls in mowed areas pre- and post-treatment, respectively. Eighteen and 49 nests were considered untreated controls in tebuthiuron-treated areas pre- and post-treatment.

treatment (0.65, 95% CI = 0.59 to 0.73). Average female survival was lower in years before treatments (0.72, 95% CI = 0.63 to 0.83) compared with years following treatment implementation (0.81, 95% CI = 0.78 to 0.85).

Nest survival

Precipitation 1 day before nest fate was negatively correlated with nest survival in mowing treatment models (Table 2). Nest survival did not differ before versus after mowing, between treatment and untreated control individuals, or treatment and off-site control individuals (Table 2). In addition, we found no evidence for an interaction between treatment and period when comparing individuals exposed to mowing treatments and untreated control or off-site control individuals (Table 2; Figure 4A).

Precipitation that occurred over the 5-day period before nest completion was the most supported environmental model of nest survival in tebuthiuron treatment models; however, 95% confidence intervals for this precipitation coefficient overlapped zero (Table 2). Nest survival was lower in years following treatment (period), and nest survival was lower for off-site control and untreated control individuals, compared with those exposed to tebuthiuron treatments. However, we found no evidence for an interaction between treatment and period when comparing individuals exposed to tebuthiuron treatment and untreated control or off-site control individuals (Table 2; Figure 4B).

Brood survival

Precipitation occurring over the previous 3 days was negatively correlated with brood survival in mowing treatment models (Table 3). Coefficient values for all other covariates overlapped zero and we found no evidence for an interaction between distance to mowing treatment and period (Table 3). For tebuthiuron models, precipitation occurring over the previous day was the most supported environmental model of brood

TABLE 2 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [UCL]) from Cox proportional hazard models evaluating environmental and treatment variables on greater sage-grouse nest survival risk in Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

	Mow				Tebuthiuron			
Parameter	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
Environmental								
Precipitation (1 day)	0.05	0.01	0.03	0.07				
Precipitation (5 days)					0.01	0.01	−0.00	0.02
Treatment[a]								
Off-site control[b]	0.09	0.29	−0.48	0.67	1.27	0.47	0.35	2.19
Untreated control	0.46	0.35	−0.23	1.15	1.22	0.52	0.21	2.24
Period[c]	0.00	0.24	−0.47	0.47	1.12	0.43	0.27	1.96
Off-site control[b] × period[c]	0.35	0.32	−0.28	0.97	−0.82	0.48	−1.76	0.11
Untreated control × period[c]	−0.48	0.43	−1.31	0.35	−0.87	0.56	−1.96	0.23

[a]Treatment nests served as the reference category.

[b]Used in nest survival models. Off-site control nests were from individuals captured in the 2 untreated study areas. The median distance of nests located in off-site control study sites to any treatment was 20.7 km (range = 10.3–28.1 km).

[c]Pre- and post-treatment. Period before treatment served as the reference category.

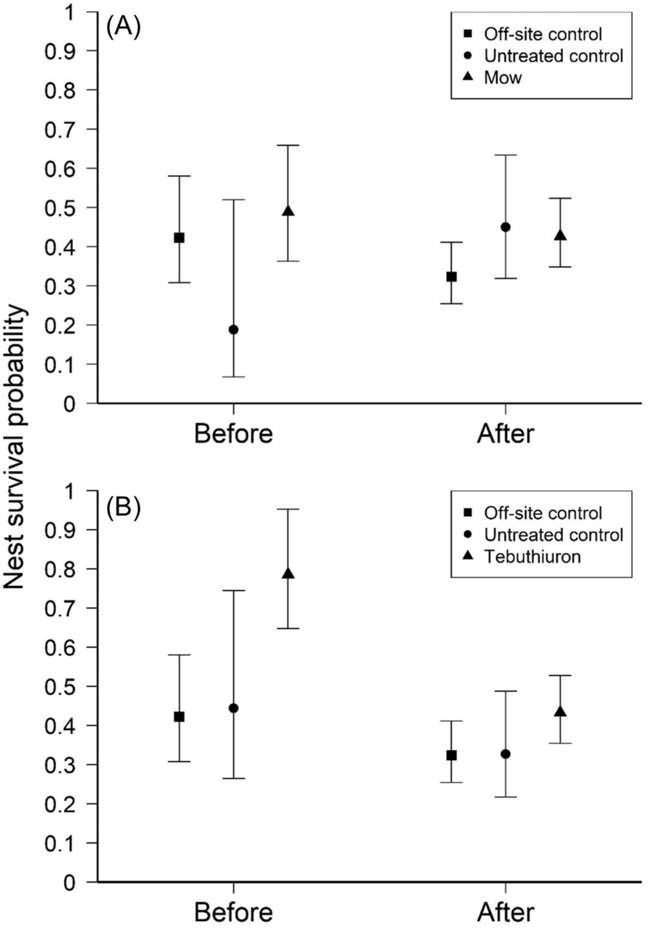

FIGURE 4 Probability of greater sage-grouse nest survival and 95% confidence intervals for nests exposed to mowing (A) and tebuthiuron (B) treatments compared to untreated control (circles) and off-site control (squares) nests during pre-treatment (2011–2013, before) and post-treatment (2014–2019, after) time periods, Fremont and Natrona counties, central Wyoming, USA.

TABLE 3 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [UCL]) from Cox proportional hazard models evaluating environmental and treatment variables on greater sage-grouse brood survival risk in Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

	Mow				Tebuthiuron			
Parameter	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
Environmental								
Precipitation (3 days)	0.03	0.02	0.00	0.07				
Precipitation (1 day)					−0.18	0.11	−0.39	0.02
Treatment								
Distance (km)	−0.00	0.00	−0.00	0.00	0.00	0.05	−0.09	0.10
Period[a]	−0.21	0.46	−1.12	0.70	0.43	0.50	−0.56	1.41
Distance × period	0.00	0.00	−0.00	0.00	0.00	0.05	−0.10	0.11

[a]Pre- and post-treatment. The before treatment period was the reference category.

survival; however, confidence intervals surrounding the coefficient estimate for precipitation overlapped zero (Table 3). Coefficient values for remaining variables in the tebuthiuron model contained 95% confidence intervals that overlapped zero and we found no evidence for an interaction between treatment and period (Table 3).

Female survival

The most supported environmental model of female survival in mowing treatment models included NDVI, but the coefficient had 95% confidence intervals overlapping zero (Table 4). Remaining coefficients in this model had 95% confidence intervals that overlapped zero and we found no evidence for an interaction between distance to mowing treatments and period (Table 4). In the tebuthiuron model, NDVI was negatively correlated with female survival (Table 4). In this analysis NDVI was the only model covariate with 95% confidence intervals that did not overlap with zero. We found no evidence for an interaction between distance to tebuthiuron treatment and period (Table 4).

Resource selection

Nest-site selection

The most supported model for nest-site selection in mowed areas included big sagebrush cover within 0.564 km, shrub height within 0.93 km, herbaceous cover within 1.6 km, bare ground at the local scale, and the distance to treatment × period interaction (Table 5). Females selected greater big sagebrush cover but lower shrub height, herbaceous cover, and bare ground (Table 6). The main effect of treatment suggested that females selected nest sites closer to mowed areas; however, the distance to treatment × period interaction term suggested that selection for mowed areas did not differ before or after treatment (Table 6).

The most supported nest-site selection model in tebuthiuron areas included selection for big sagebrush cover at the local scale, bare ground within 0.564 km, and the distance to treatment × period interaction (Table 5). Females selected nest sites closer to tebuthiuron treatments, but we did not find evidence for an interaction between distance to treatment and period (Table 6), suggesting that selection for tebuthiuron treatments did not differ before or after treatments.

TABLE 4 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [UCL]) from Cox proportional hazard models evaluating environmental and treatment variables on greater sage-grouse female survival risk in Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

	Mow				Tebuthiuron			
Parameter	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
Environmental								
NDVI[a]	−1.40	1.76	−4.83	2.07	4.02	1.93	0.23	7.81
Treatment								
Distance (km)	−0.01	0.02	−0.04	0.03	0.03	0.04	−0.04	0.10
Period[b]	−0.31	0.34	−0.97	0.36	−0.22	0.58	−1.36	0.93
Distance × period[b]	0.00	0.02	−0.04	0.05	−0.01	0.04	−0.09	0.07

[a]Normalized difference vegetation index.

[b]Pre- and post-treatment. The before treatment period was the reference category.

TABLE 5 Models explaining greater sage-grouse nest, brood, and female habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, Fremont and Natrona counties, central Wyoming, USA, 2011–2019. We used the number of parameters (*K*), change in corrected Akaike's Information Criterion score from the top model (ΔAIC_c), and Akaike weights (w_i) to evaluate model fit for sage-grouse habitat selection.

Model[a,b]	*K*	ΔAIC_c	w_i
Nest			
Mow (base model: $Bsage_{564}$ + shrub $height_{930}$ + $herb_{1600}$ + $bare_{30}$)			
Base model + distance to treatment × period	10	0.00	0.63
Base model + $treatment_{335}$ × period	10	1.96	0.24
Base model + $treatment_{564}$ × period	10	3.42	0.11
Base model + $treatment_{930}$ × period	10	7.45	0.02
Base model + $treatment_{1600}$ × period	10	10.36	0.00
Base model	7	14.71	0.00
Null (individual + site)	3	213.03	0.00
Tebuthiuron (base model: $Bsage_{30}$ + $bare_{564}$)			
Base model + distance to treatment × period	8	0.00	0.96
Base model + $treatment_{1600}$ × period	8	6.23	0.04
Base model + $treatment_{930}$ × period	8	13.05	0.00
Base model + $treatment_{564}$ × period	8	15.26	0.00
Base model + $treatment_{335}$ × period	8	17.10	0.00
Base model	5	22.25	0.00
Null (individual + site)	3	33.85	0.00
Brood			
Mow (base model: $bare_{30}$ + $herb_{335}$ + $slope_{30}$)			
Base model + distance to treatment × period	9	0.00	1.00
Base model + $treatment_{335}$ × period	9	32.32	0.00
Base model + $treatment_{564}$ × period	9	33.10	0.00
Base model + $treatment_{930}$ × period	9	34.92	0.00
Base model + $treatment_{1600}$ × period	9	40.84	0.00
Base model	6	52.78	0.00
Null (individual + site)	3	399.42	0.00
Tebuthiuron (base model: $bare_{30}$ + shrub $height_{30}$ + $slope_{1600}$)			
Base model + distance to treatment × period	9	0.00	1.00
Base model + $treatment_{1600}$ × period	9	32.15	0.00
Base model + $treatment_{930}$ × period	9	35.16	0.00
Base model + $treatment_{564}$ × period	9	35.72	0.00
Base model + $treatment_{335}$ × period	9	35.92	0.00
Base model	6	46.59	0.00
Null (individual + site)	3	337.82	0.00

(Continues)

TABLE 5 (Continued)

Model[a,b]	*K*	ΔAIC_c	w_i
Female			
Mow (base model: shrub $height_{335}$ + $bare_{30}$ + $herb_{335}$ + $slope_{335}$)			
Base model + distance to treatment × period	10	0.00	1.00
Base model + $treatment_{564}$ × period	10	18.85	0.00
Base model + $treatment_{335}$ × period	10	19.79	0.00
Base model + $treatment_{930}$ × period	10	26.45	0.00
Base model + $treatment_{1600}$ × period	10	28.67	0.00
Base model	7	71.02	0.00
Null (individual + site)	3	1,059.09	0.00
Tebuthiuron (base model: $Bsage_{30}$ + shrub $height_{30}$ + $bare_{30}$ + $slope_{1600}$)			
Base model + distance to treatment × period	10	0.00	1.00
Base model + $treatment_{1600}$ × period	10	153.76	0.00
Base model + $treatment_{930}$ × period	10	201.57	0.00
Base model + $treatment_{564}$ × period	10	213.11	0.00
Base model + $treatment_{335}$ × period	10	215.72	0.00
Base model	7	262.24	0.00
Null (individual + site)	3	1,020.67	0.00

[a]Parameters include bare ground cover (bare; %), big sagebrush cover (Bsage), herbaceous cover (herb; %), slope (%), shrub height (cm), distance to treatment (km), amount of treatment (treatment; ha), and period (before or after treatment).
[b]Subscripts for predictor variables correspond to the 30-m raster cell (30) and 4 circular analysis regions: 0.335-km radii (335), 0.564-km radii (564), 0.930-km radii (930), and 1.6-km radii (1600).

Brood habitat selection

In mowed areas, base models suggested that brood-rearing females avoided bare ground and selected lower slopes at the local scale (Tables 5 and 7). The most supported brood resource selection base model in tebuthiuron areas included avoidance of bare ground at the local scale, selection for greater shrub height at the local scale, and selection for lower slope within 1.6 km (Tables 5 and 7). Females with broods used areas closer to mowed and tebuthiuron treatment areas (Table 7), but we did not detect a pre- or post-treatment interaction for distance to treatment in brood-rearing habitat selection at either mowed or tebuthiuron treatment areas (Table 7).

Female habitat selection

Females selected greater shrub height within 0.335 km, avoided bare ground at the local scale, and selected lower slopes within 0.335 km in mowed areas (Tables 5 and 8). The main effect of treatment suggested that females selected areas closer to mowed treatments (Table 8). However, the treatment × period interaction suggested that selection for treatments varied before and after treatment, with evidence for avoidance of mowed treatments after implementation (Table 8; Figure 5).

TABLE 6 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [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, Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

Parameter[a,b]	Estimate	SE	LCL	UCL
Mow				
$Bsage_{564}$	0.39	0.05	0.31	0.49
Shrub $height_{930}$	−0.08	0.02	−0.12	−0.04
$Herb_{1600}$	−0.18	0.06	−0.31	−0.06
$Bare_{30}$	−0.04	0.01	−0.06	−0.02
Distance to treatment	−0.36	0.10	−0.56	−0.17
Period	−0.32	0.23	−0.78	0.14
Distance to treatment × period	0.19	0.11	−0.02	0.40
Tebuthiuron				
$Bsage_{30}$	0.06	0.02	0.02	0.09
$Bare_{564}$	0.03	0.01	0.01	0.05
Distance to treatment	−0.47	0.20	−0.86	−0.07
Period	−0.07	0.31	−0.68	0.54
Distance to treatment × period	0.09	0.22	−0.35	0.52

[a]Parameters include bare ground cover (bare; %), big sagebrush cover (Bsage), herbaceous cover (herb; %), shrub height (cm), distance to treatment (km), and period (before or after treatment).

[b]Subscripts for predictor variables correspond to the 30-m raster cell (30) and 4 circular analysis regions: 0.335-km radii (335), 0.564-km radii (564), 0.930-km radii (930), and 1.6-km radii (1600).

The most supported female habitat selection base model in tebuthiuron areas included avoidance of big sagebrush cover and bare ground at the local scale, selection for shrub height at the local scale, and selection for flatter slopes within 1.6 km (Tables 5 and 8). Females used areas closer to tebuthiuron treatments (Table 8) before and after treatment implementation. We did not find evidence for an interaction with distance to treatment period (Table 8), suggesting that female selection for treatments did not change following tebuthiuron application.

Vegetation response

Mowing treatments

The cover of Wyoming big sagebrush differed between treated and untreated control sites ($F_{1,38}$ = 25.25, P < 0.01) and year ($F_{5,183}$ = 3.91, P < 0.01). We did not find evidence for a treatment × year interaction ($F_{5,183}$ = 0.28, P = 0.49), however. Mowed sites had lower Wyoming big sagebrush cover than untreated control sites during each study year following treatments (Figure 6A). We found differences in Wyoming big sagebrush height between treated and untreated control sites ($F_{1,38}$ = 50.42, P < 0.01) and year ($F_{5,183}$ = 3.97, P < 0.01), and this relationship was consistent across years ($F_{5,278}$ = 1.60, P = 0.16). Wyoming big sagebrush height was consistently greater at untreated control sites compared to mowing sites during each year following treatments (Figure 6B).

TABLE 7 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [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, Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

Parameter[a,b]	Estimate	SE	LCL	UCL
Mow				
$Bare_{30}$	−0.07	0.01	−0.08	−0.06
$Herb_{335}$	−0.01	0.01	−0.03	0.02
$Slope_{30}$	−0.04	0.01	−0.05	−0.02
Distance to treatment	−0.24	0.05	−0.35	−0.14
Period	−0.14	0.16	−0.45	0.17
Distance to treatment × period	0.07	0.06	−0.05	0.18
Tebuthiuron				
$Bare_{30}$	−0.06	0.00	−0.07	−0.05
Shrub $height_{30}$	0.01	0.00	0.00	0.02
$Slope_{1600}$	−0.10	0.02	−0.13	−0.06
Distance to treatment	−0.30	0.08	−0.46	−0.14
Period	0.04	0.16	−0.27	0.35
Distance to treatment × period	−0.02	0.10	−0.21	0.16

[a]Parameters include bare ground cover (bare; %), herbaceous cover (herb; %), slope (%), shrub height (cm), distance to treatment (km), and period (before or after treatment).

[b]Subscripts for predictor variables correspond to the 30-m raster cell (30) and 4 circular analysis regions: 0.335-km radii (335), 0.564-km radii (564), 0.930-km radii (930), and 1.6-km radii (1600).

Perennial grass cover did not differ between treated and untreated control sites ($F_{1,38} = 3.82$, $P < 0.06$). A significant year effect ($F_{5,183} = 26.33$, $P < 0.01$) and treatment × year interaction ($F_{10,278} = 2.72$, $P = 0.02$) suggested that perennial grass cover exhibited yearly variation across treatment types and was lowest at both untreated control and treatment sites during 2018 and 2019 (Figure 7A). Perennial grass height did not differ between treated and untreated control sites ($F_{1,38} = 0.28$, $P = 0.60$). Differences across years ($F_{5,183} = 90.52$, $P < 0.01$) and a significant treatment × year interaction ($F_{5,183} = 2.87$, $P = 0.02$), suggested that perennial grass height exhibited yearly variation, with the lowest height occurring at untreated control and treatment sites during 2016 and 2019 (Figure 7B).

Forb cover varied annually ($F_{5,183} = 12.95$, $P < 0.01$) but not between treated and untreated control sites ($F_{1,38} = 2.85$, $P = 0.1$), or by year (treatment × year interaction; $F_{5,183} = 1.46$, $P = 0.2$). Forb cover was not greater at mowing sites compared to untreated control sites in any year following treatment (Figure 8A). Forb species richness was similar at treated and untreated control sites ($F_{1,38} = 0.48$, $P = 0.49$), varied by year ($F_{5,183} = 13.62$, $P < 0.01$), and differed by the treatment × year interaction ($F_{10,183} = 3.15$, $P < 0.01$). Forb species richness did not differ between mowing and untreated control sites during each year but varied across years (Figure 8B).

Tebuthiuron treatments

Wyoming big sagebrush cover did not differ between treated and untreated control sites ($F_{1,38} = 0.45$, $P = 0.51$). Big sagebrush cover differed across years ($F_{5,190} = 21.72$, $P < 0.01$) and we found evidence for a treatment × year

TABLE 8 Variable coefficients, standard errors (SE), and 95% confidence intervals (lower [LCL] and upper confidence limits [UCL]) from models evaluating environmental and treatment variables on female greater sage-grouse habitat selection relative to mowing and tebuthiuron treatments in Wyoming big sagebrush, Fremont and Natrona counties, central Wyoming, USA, 2011–2019.

Parameter[a,b]	Estimate	SE	LCL	UCL
Mow				
Shrub $height_{335}$	0.01	0.00	0.00	0.02
$Bare_{30}$	−0.04	0.00	−0.05	−0.04
$Herb_{335}$	−0.00	0.01	−0.02	0.01
$Slope_{335}$	−0.06	0.01	−0.07	−0.05
Distance to treatment	−0.17	0.02	−0.21	−0.12
Period	−0.26	0.07	−0.40	−0.12
Distance to treatment × period	0.11	0.02	0.06	0.16
Tebuthiuron				
$Bsage_{30}$	−0.02	0.00	−0.03	−0.01
Shrub $height_{30}$	0.01	0.00	0.00	0.01
$Bare_{30}$	−0.04	0.00	−0.04	−0.03
$Slope_{1600}$	−0.15	0.01	−0.17	−0.13
Distance to treatment	−0.41	0.05	−0.50	−0.32
Period	−0.10	0.08	−0.27	0.06
Distance to treatment × period	0.09	0.05	−0.01	0.19

[a]Parameters include big sagebrush cover (Bsage; %), shrub height (cm), bare ground cover (bare; %), herbaceous cover (herb; %), slope (%), distance to treatment (km), and period (before or after treatment).

[b]Subscripts for predictor variables correspond to the 30-m raster cell (30) and 4 circular analysis regions: 0.335-km radii (335), 0.564-km radii (564), 0.930-km radii (930), and 1.6-km radii (1600).

interaction ($F_{5,190} = 7.49$, $P < 0.01$). Sites treated with tebuthiuron had greater Wyoming big sagebrush cover compared with untreated control areas immediately after treatment in 2014 but lower cover in subsequent years (Figure 6C). The height of sagebrush did not vary between treated and untreated sites ($F_{1,38} = 0.05$, $P = 0.83$). Sagebrush height differed across years ($F_{5,190} = 20.29$, $P < 0.01$), but this relationship was similar across years ($F_{5,190} = 0.59$, $P < 0.71$). Wyoming big sagebrush height was similar at tebuthiuron and untreated control sites during each study year (Figure 6D).

Perennial grass cover differed across treatment types ($F_{1,38} = 4.51$, $P = 0.04$) and years ($F_{5,190} = 12.75$, $P < 0.01$); however, we found no evidence for a treatment × year interaction ($F_{5,190} = 0.54$, $P = 0.74$), suggesting that perennial grass cover exhibited yearly variation across treatment types (Figure 7C). Perennial grass height also differed by treatment ($F_{1,38} = 5.12$, $P = 0.03$) and years ($F_{5,190} = 76.14$, $P < 0.01$), but we found no evidence for a treatment × year interaction ($F_{5,190} = 1.25$, $P = 0.29$; Figure 7D).

Forb cover did not differ across treatment sites ($F_{1,38} = 0.80$, $P = 0.38$). Forb cover differed across years ($F_{5,190} = 10.94$, $P < 0.01$); however, we did not detect a treatment × year interaction ($F_{5,190} = 0.77$, $P = 0.57$; Figure 8C). Forb species richness did not differ between treatment sites ($F_{1,38} = 0.13$, $P = 0.72$) but differed across years ($F_{5,190} = 6.16$, $P < 0.01$). We did not detect a treatment × year interaction for forb species richness ($F_{5,190} = 0.75$, $P = 0.59$; Figure 8D).

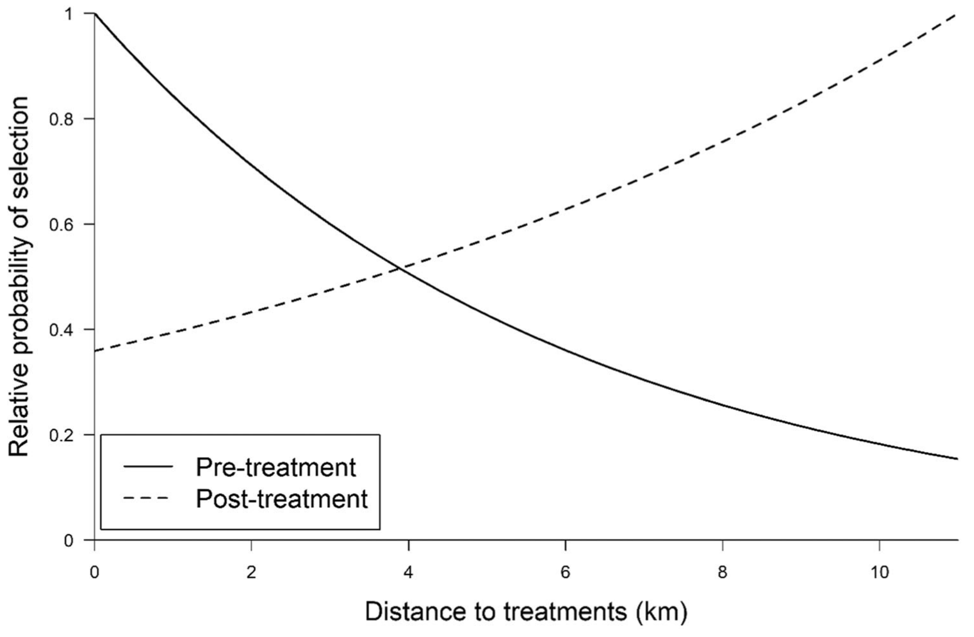

FIGURE 5 Relative probability of greater sage-grouse habitat selection during pre-treatment (2011–2013; solid line) and post-treatment (2014–2019; dashed line) time periods in relation to distance to mowing treatments, Fremont and Natrona counties, central Wyoming, USA, 2011–2019. We standardized relative probability of selection by dividing predicted values by their maximum.

Mowing treatments compared with exclosures

Perennial grass cover varied annually ($F_{5,141}$ = 21.02, P < 0.01) but not across treatments ($F_{2,29}$ = 3.13, P = 0.06) and exhibited annual variation across treatment types (Figure 9A; treatment × year interaction; $F_{10,141}$ = 2.75, P < 0.01). Perennial grass height varied by treatment type ($F_{2,29}$ = 5.51, P < 0.01) and year ($F_{5,141}$ = 66.20, P < 0.01), and exhibited yearly variation across treatments, evidenced by a significant treatment × year interaction ($F_{10,141}$ = 6.54, P < 0.01; Figure 9B). However, perennial grass cover and height did not differ between mowing treated sites, temporary exclosures, or permanent exclosures in any years following the removal of fencing at temporary exclosure locations.

Forb cover did not vary by treatment type ($F_{2,29}$ = 0.25, P = 0.78) but varied annually ($F_{5,141}$ = 10.74, P < 0.01). We did not find evidence for a treatment × year interaction ($F_{10,141}$ = 0.91, P = 0.52; Figure 10A). Forb species richness did not differ across treatments ($F_{2,29}$ = 0.24, P = 0.79) but differed annually ($F_{5,141}$ = 14.24, P < 0.01). We found no evidence for a treatment × year interaction ($F_{10,141}$ = 0.94, P = 0.50; Figure 10B). There were no differences in forb cover or forb species richness between mowing treated sites, temporary exclosures, or permanent exclosures in any years following the removal of temporary exclosures.

Tebuthiuron treatments compared with exclosures

Perennial grass cover differed across treatment types ($F_{2,29}$ = 3.42, P = 0.05), and annually ($F_{5,145}$ = 4.73, P < 0.01), but we found no evidence for a treatment × year interaction ($F_{10,145}$ = 1.30, P = 0.24; Figure 9C). Perennial grass height did not differ across types ($F_{2,29}$ = 2.90, P = 0.07) but differed across years ($F_{5,145}$ = 50.23, P < 0.01) and we found evidence for a treatment × year interaction ($F_{10,145}$ = 4.13, P < 0.01), suggesting that perennial grass height

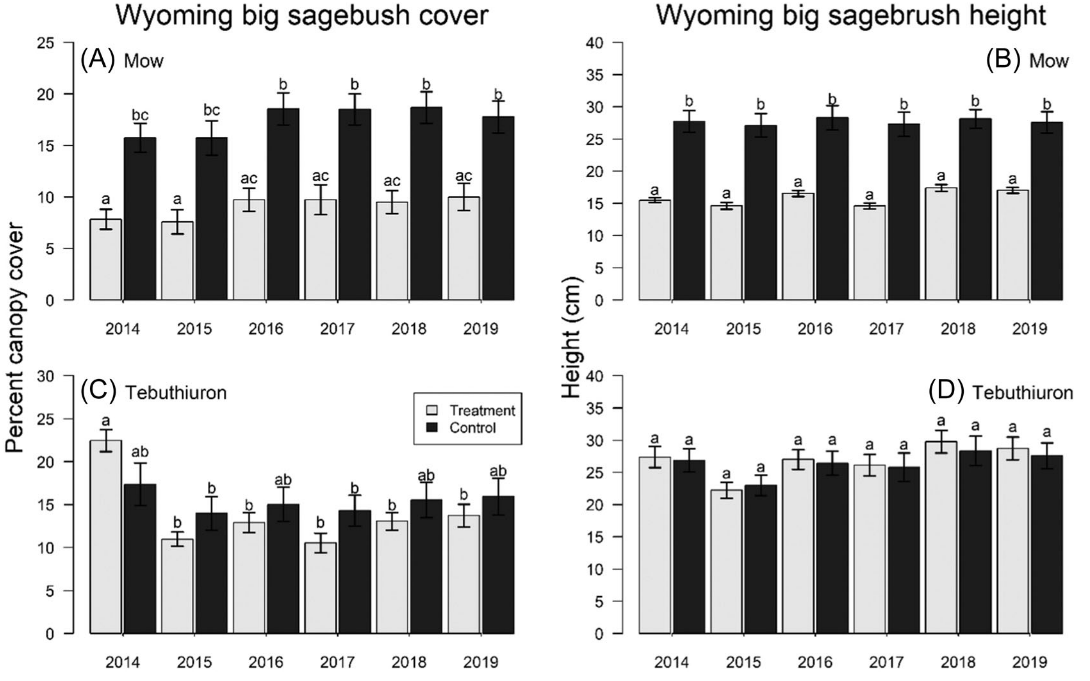

FIGURE 6 Mean (±SE) Wyoming big sagebrush cover and height at mowing (A, B) and tebuthiuron-treated (C, D) sites compared to untreated control sites adjacent to treatments in Fremont and Natrona counties, central Wyoming, USA, 2014–2019. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

exhibited yearly variation across sites (Figure 9D). Perennial grass cover and height did not differ between tebuthiuron-treated sites, temporary exclosures, or permanent exclosures in years following the removal of fencing at temporary exclosure locations.

Forb cover did not differ across types ($F_{2,29} = 0.15$, $P = 0.86$) but differed across years ($F_{5,145} = 8.37$, $P < 0.01$). We found no evidence for a treatment × year interaction ($F_{10,145} = 1.04$, $P = 0.41$; Figure 10C). Forb species richness did not differ across types ($F_{2,29} = 0.04$, $P = 0.96$) but differed across years ($F_{5,145} = 5.63$, $P < 0.01$) and we found evidence for a treatment × year interaction ($F_{10,145} = 2.43$, $P = 0.01$), suggesting that forb species richness exhibited yearly variation across sites (Figure 10D). However, there were no differences in forb cover or forb species richness between tebuthiuron-treated sites, temporary exclosures, or permanent exclosures in years following the removal of temporary exclosure fencing.

Forb and invertebrate dry matter

Forb DM differed between mowed and untreated control plots ($F_{1,38} = 7.12$, $P = 0.01$) and year ($F_{4,152} = 89.12$, $P < 0.01$), with the greatest forb DM at untreated control sites during 2017 (Figure 11A). Forb DM did not differ between tebuthiuron and control plots ($F_{1,38} = 0.01$, $P = 0.91$) but differed by year ($F_{4,152} = 60.85$, $P < 0.01$) with the greatest forb DM during 2017 (Figure 11C). In all years except 2017, forb DM did not differ between treated plots and untreated controls at mowing or tebuthiuron sites.

Invertebrate DM differed yearly at mowed and untreated control sites ($F_{4,152} = 44.35$, $P < 0.01$) with the greatest invertebrate DM during 2014 (Figure 11B), but DM did not vary by treatment type ($F_{1,38} = 0.27$, $P = 0.61$).

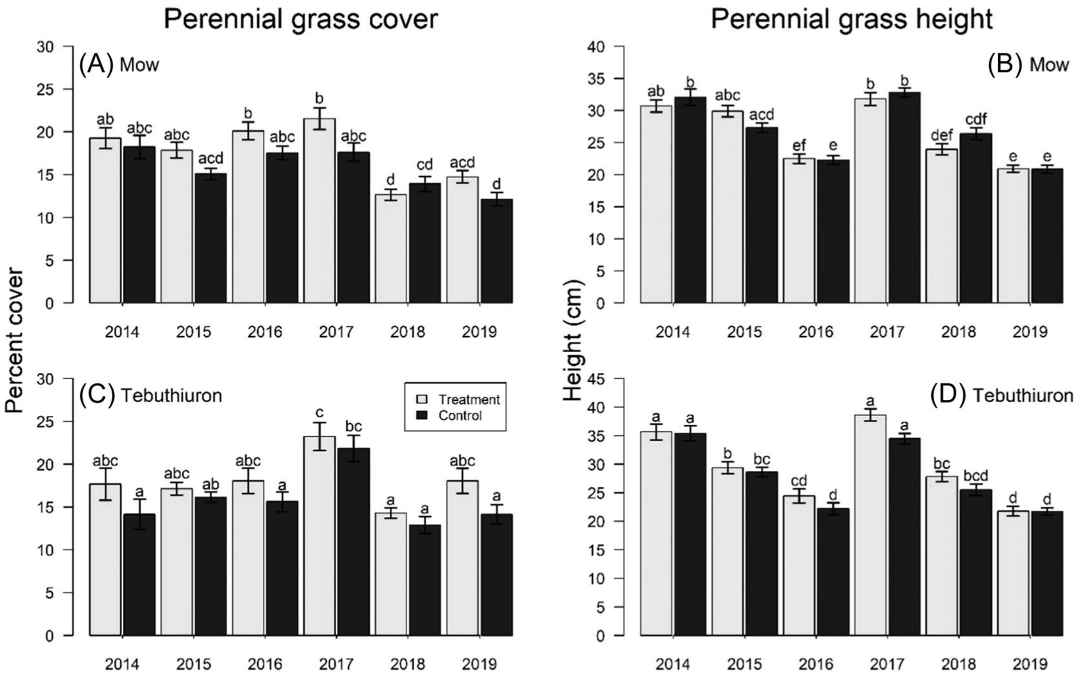

FIGURE 7 Mean (±SE) perennial grass cover and height at mowing (A, B) and tebuthiuron-treated (C, D) sites compared to untreated control sites adjacent to treatments in Fremont and Natrona counties, central Wyoming, USA, 2014–2019. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

Similarly, invertebrate DM did not differ between tebuthiuron and untreated control plots ($F_{1,38} = 0.93$, $P = 0.34$) but differed across years ($F_{4,152} = 36.73$, $P < 0.01$) with the greatest invertebrate DM during 2014 (Figure 11D). Invertebrate DM did not differ between treated plots and untreated control plots at mowing or tebuthiuron sites in any years following treatments.

DISCUSSION

Treatments in big sagebrush aimed at enhancing habitats for sagebrush-associated wildlife, including the greater sage-grouse, have occurred for decades. Yet the fitness and fine-scale resource selection responses of sage-grouse to sagebrush reduction treatments have not been evaluated rigorously. We experimentally investigated resource selection and demography of sage-grouse in relation to 2 types of sagebrush reduction treatments, mowing and tebuthiuron application. Neither mowing nor tebuthiuron treatments influenced nest success, brood success, or female survival. Moreover, sage-grouse did not select habitats based on mowing and tebuthiuron treatments. For each life stage we evaluated, sage-grouse selected areas closer to treatment areas before treatments were implemented, confirming that treated areas were used by sage-grouse during the breeding season. However, patterns of habitat selection did not vary following sagebrush treatments. Our results therefore provided no evidence that areas that were mowed or treated with tebuthiuron improved reproductive success, increased survival, or are preferred by sage-grouse in breeding habitats dominated by Wyoming big sagebrush. Our conclusions are corroborated by the lack of positive response of herbaceous cover and productivity of forbs and insects in treated areas compared with untreated control sites.

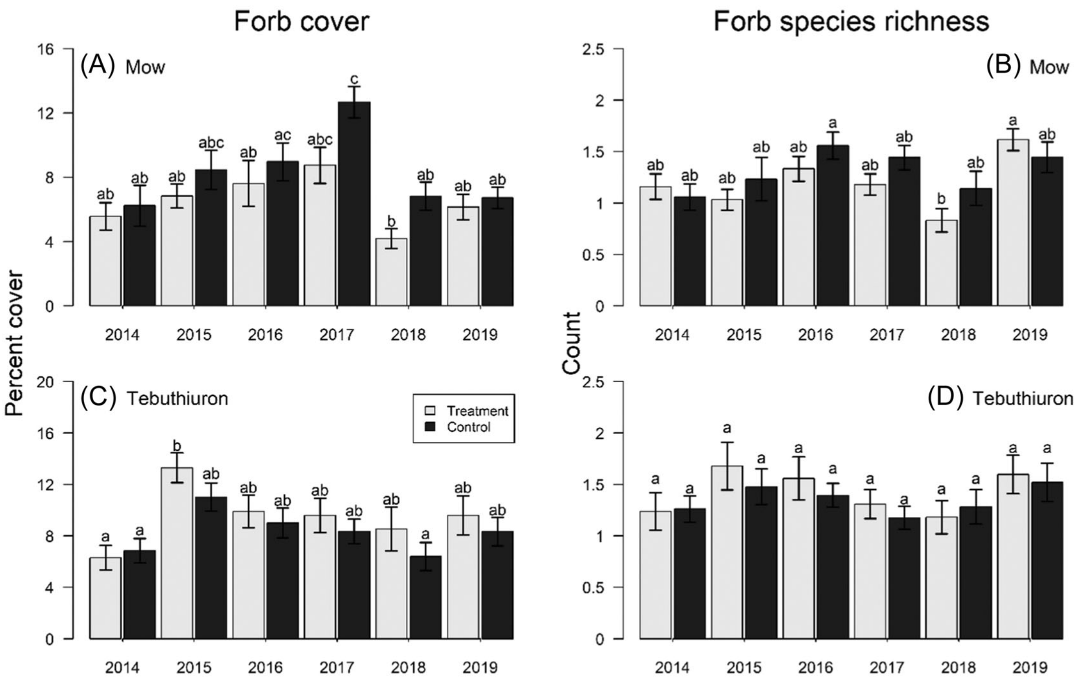

FIGURE 8 Mean (±SE) forb cover and forb species richness at mowing (A, B) and tebuthiuron-treated (C, D) sites compared to untreated control sites adjacent to treatments in Fremont and Natrona counties, central Wyoming, USA, 2014–2019. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

To be beneficial to sage-grouse populations, treatments should improve habitat conditions conducive to increasing adult and chick survival, nest success, or a combination of these demographic rates. However, implementing treatments designed to reduce sagebrush cover for a sagebrush-obligate species is counterintuitive. Numerous studies have demonstrated the importance of structural cover of sagebrush used yearlong by sage-grouse for concealment. Management guidelines for sage-grouse suggest 10–25% sagebrush cover and 40–80 cm sagebrush height is needed for nesting and early brood-rearing habitats (Connelly et al. 2000*b*). Females also may select nesting locations based on the 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). Mean height of nest shrubs was approximately 40 cm across 5 study areas in central and southwestern Wyoming, including our study area (Dinkins et al. 2016). Selection for areas with intermediate visual obstruction from all cover (i.e., a quadratic relationship) by early brood-rearing females in our study area also corroborate guidelines and findings from other studies (Smith et al. 2018*a*). We found that mowing treatments reduced sagebrush cover and height compared with untreated control sites. Following mowing treatments, moreover, the reduction in cover and height remained similar for the duration of our study, which is consistent with the slow recovery time of sagebrush (Wambolt and Payne 1986).

Provided that adequate sagebrush cover remains for concealment, increasing herbaceous understory would signify a positive response following treatments. Whereas grass height may have no consistent relationship with sage-grouse nest survival (Smith et al. 2020), greater grass cover and height are selected during nesting and brood-rearing (Hagen et al. 2007, Kirol et al. 2012, Gibson et al. 2016), presumably to provide additional concealment cover over what is provided by shrubs alone. We found no differences between perennial grass cover and height at either mowed or tebuthiuron-treated sites compared to respective control sites, suggesting that reduction in sagebrush cover at treated sites was not offset by an increase in perennial grass cover. The response patterns we observed in vegetation structure,

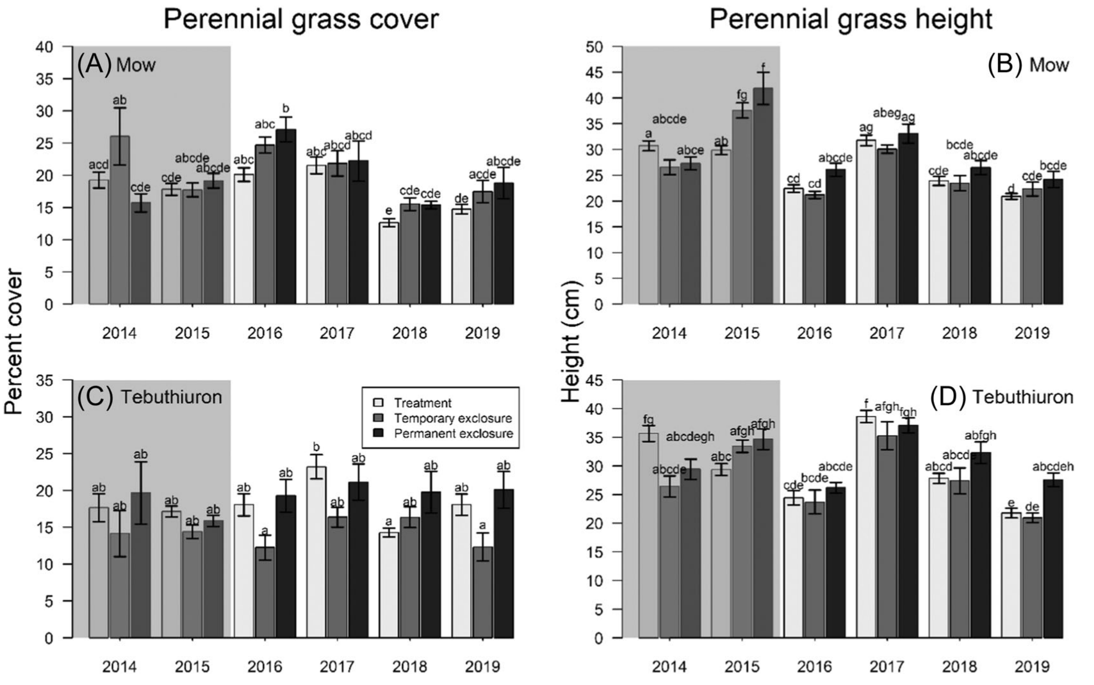

FIGURE 9 Mean (±SE) perennial grass cover and height at mowing (A, B) and tebuthiuron-treated (C, D) sites, temporary exclosures, and permanent exclosures before (2014–2015; gray) and after (2016–2019) removal of temporary exclosures in Fremont and Natrona counties, central Wyoming, USA. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

moreover, were similar to those documented by other studies focused on treatments in Wyoming big sagebrush. Increased herbaceous cover following mowing treatments in Wyoming big sagebrush in Oregon, for example, were primarily from undesirable species such as cheatgrass and nonnative forbs (Davies et al. 2012*b*). Perennial grass height and cover in north-central Wyoming did not vary between mowing treatments and reference sites in Wyoming big sagebrush up to 9 years after treatment (Hess and Beck 2012). Because treatments, and mowing treatments in particular, reduced sagebrush cover and height to levels lower than sage-grouse use for nesting, and perennial grass cover and height did not differ from untreated controls, treated areas may not provide suitable nesting or early brood-rearing habitat until treated sagebrush recovers to sufficient levels. Any short-term benefits of treatments would therefore most likely occur if treatments increased foraging opportunities for sage-grouse.

During spring growth, forbs have greater nutritional quality than sagebrush leaves and may contribute up to 50% of pre-laying sage-grouse diets (Barnett and Crawford 1994, Gregg et al. 2008). The nutritional condition of females is important for egg development and quality. Greater forb availability near nests can positively influence reproductive success for sage-grouse (Gibson et al. 2016). In addition, availability of forbs and invertebrates are critical for sage-grouse chick survival (Johnson and Boyce 1990). A failure of treatments to increase forb and invertebrate production in treated Wyoming big sagebrush (Hess and Beck 2014, Smith et al. 2019*b*, this study) supports our finding of a neutral demographic response and lack of selection of treatments. We found no differences in forb cover or forb species richness between mowing or tebuthiuron treatments and untreated sites during each year following treatments. In addition, forb DM did not differ between treatment types or between treated and untreated areas up to 4 years after treatments occurred (Smith et al. 2019*b*), and we found no differences in forb DM 5 years after treatments in 2018. Forb cover and production typically return to pre-treatment conditions within 1–5 years (Peek et al. 1979, Fischer et al. 1996). In contrast, forb cover responded

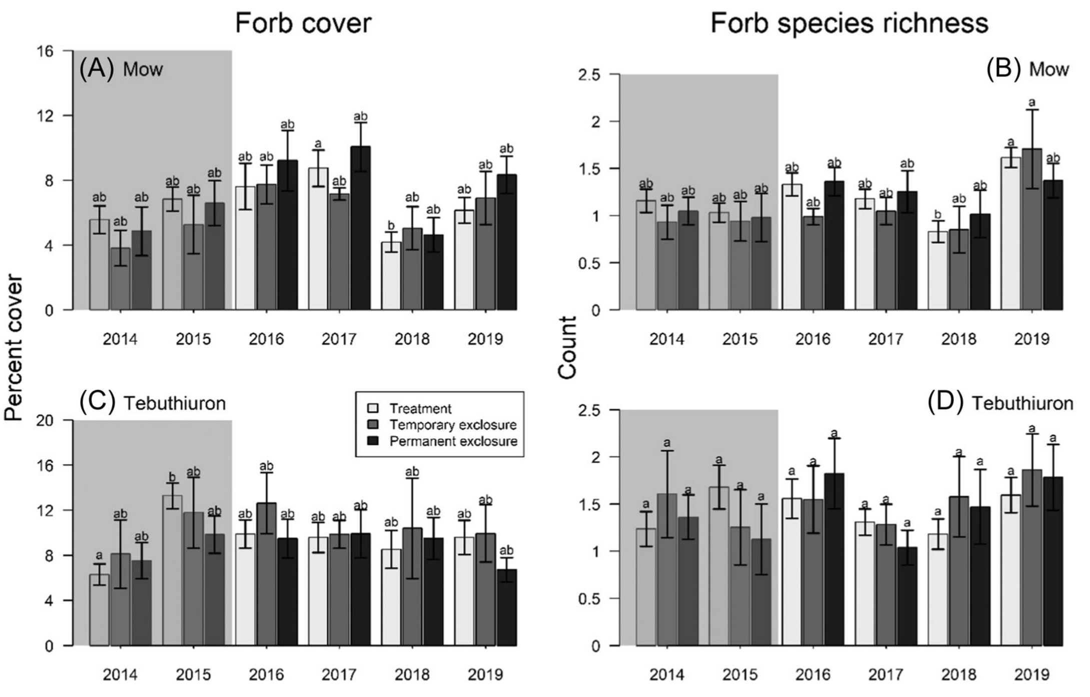

FIGURE 10 Mean (±SE) forb cover and forb species richness at mowing (A, B) and tebuthiuron-treated (C, D) sites, temporary exclosures, and permanent exclosures before (2014–2015; gray) and after (2016–2019) removal of temporary exclosures in Fremont and Natrona counties, central Wyoming, USA. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

positively to tebuthiuron treatments in mountain big sagebrush (Dahlgren et al. 2006), indicating that generalizing between treatments in Wyoming and mountain big sagebrush communities should be avoided.

Heterogeneity in vegetation can increase insect abundance and diversity (Dennis et al. 1998, Wenninger and Inouye 2008). Vegetation manipulation is therefore likely to influence the invertebrate community. In contrast, we found that invertebrate biomass did not differ between treatment types or between treated and untreated areas up to 5 years after treatments occurred (Smith et al. 2019*b*, this study). Our invertebrate biomass results were consistent with other studies in mountain big sagebrush (Pyle and Crawford 1996) and Wyoming big sagebrush (Fischer et al. 1996, Rhodes et al. 2010). The abundance of ants in southeastern Idaho, USA, decreased during the second and third years following prescribed burns compared with reference areas (Fischer et al. 1996). Ants positively responded to 1-year-old burns before returning to 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 with control areas (Rhodes et al. 2010). No positive response in insect biomass was detected following burning or mowing treatments in Wyoming big sagebrush communities in Wyoming (Hess and Beck 2014). Moreover, studies that have detected differences in insect abundance following disturbances in mountain big sagebrush (Nelle et al. 2000) and Wyoming big sagebrush (Rhodes et al. 2010) indicate that these differences were not biologically significant.

Livestock grazing is a widespread land use across western North America and could therefore influence the response of vegetation to treatments. Improperly managed grazing can negatively affect sagebrush plant communities (Davies et al. 2011), which could potentially offset any increases in herbaceous cover following treatments. This concern is recognized by agencies responsible for managing sagebrush (BLM 2015) and has been adopted in the WGFD protocol for treating sagebrush (WGFD 2011, 2019). We found no evidence that perennial

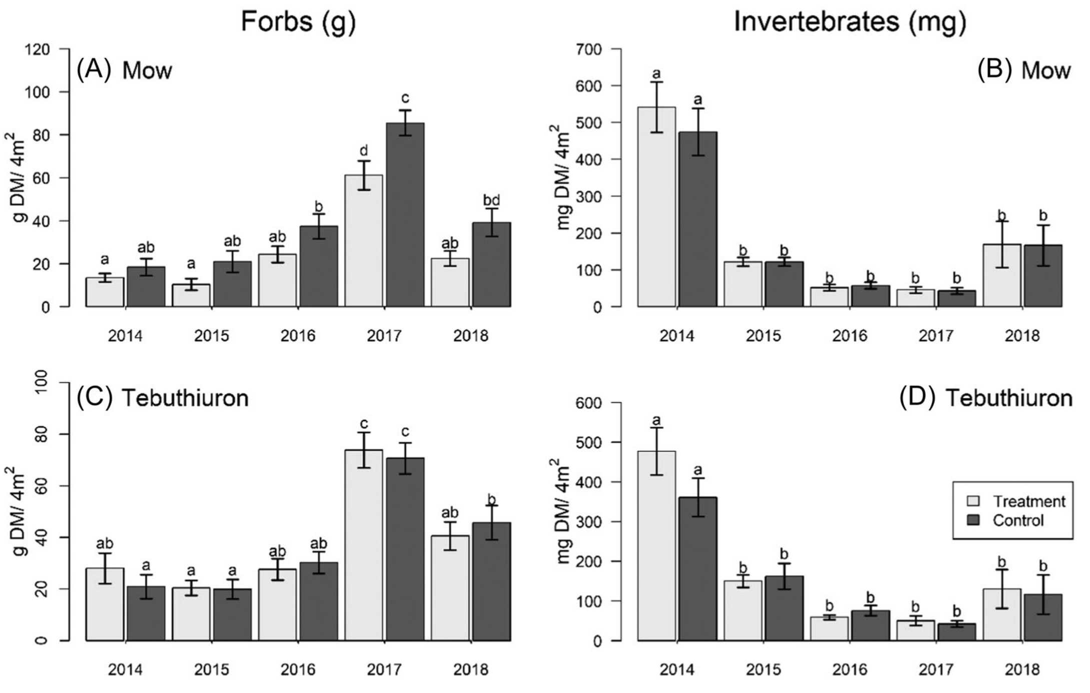

FIGURE 11 Mean (±SE) forb (g dry matter [DM]/4 m^2) and invertebrate (mg DM/4 m^2) production at mowing (A and B) and tebuthiuron (C and D) treatments compared with untreated control plots sampled during 2014–2018, Fremont and Natrona counties, central Wyoming, USA. Within each panel, means marked with the same letter do not differ (Tukey's honestly significant difference test $P > 0.05$).

grass cover, perennial grass height, forb cover, or forb species richness differed among mowed or tebuthiuron-treated areas that received 0, 2, or 6 years of grazing rest. Herbaceous cover also did not differ up to 4 years following treatment between grazed and ungrazed Wyoming big sagebrush sites that were treated with prescribed fire in Oregon (Bates et al. 2009). Therefore, our results suggest that livestock grazing is unlikely to negatively affect the response of herbaceous cover to treatments in areas with similar vegetation communities, climatic conditions, and stocking rates observed in our study.

Another potential drawback to sagebrush treatments can be negative consequences for other co-occurring species of conservation concern. There is relatively little information on other species responses to treatments in Wyoming big sagebrush (Beck et al. 2012). However, in our study system, Carlisle et al. (2018) found neutral or negative impacts of mowing treatments on Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*). 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 areas after treatment. In contrast, sagebrush-generalist species (e.g., vesper sparrow [*Pooecetes gramineus*]) may have positive or neutral responses to fine-scale mowing treatments (Carlisle et al. 2018). Avian species in other systems also have exhibited mixed responses to vegetation treatments. For example, northern bobwhite quail selected treated areas on a reclaimed surface mine (Brooke et al. 2015). However, nest success and survival of northern bobwhite was similar between areas treated with prescribed fire and untreated areas, but survival varied seasonally in response to prescribed fire (Peters et al. 2015). Increased use of burned and mowed sites by capercaillie (*Tetrao urogallus*) in Britain was attributed to an increase in preferred cover that resulted from treatments (Hancock et al. 2011) and grassland specialist birds responded positively to shrub removal with herbicides (Coffman et al. 2014).

Our study investigated short-to-mid-term local-scale responses of sage-grouse to sagebrush manipulation in Wyoming big sagebrush. Landscape-scale research occurring over a longer time period, however, also support our conclusion that treatments in Wyoming big sagebrush do not positively influence sage-grouse populations. Mechanical treatments were predictive of sage-grouse population declines in Wyoming up to 11 years after treatment, although 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. Moreover, differences in survival rates across seasons in treated areas may be an important consideration for sage-grouse. Although we found evidence for a neutral response to mowing and tebuthiuron treatments during the breeding season, sage-grouse also rely on sagebrush for food and cover during winter (Wallestad and Eng 1975). Reduction in cover and even subtle changes in the nutritional quality of sagebrush could therefore decrease winter habitat quality for sage-grouse (Davies et al. 2009). There is strong evidence that the nutritional quality of the diet is an important driver of shrub selection by sage-grouse during winter (e.g., Frye et al. 2013). In our study system, slight increases in crude protein concentrations in sagebrush leaves during winters following treatments were detected; however, marginal increases in crude protein are unlikely to improve winter habitat quality (Smith et al. 2018*b*). Given a general lack of known sage-grouse use areas during winter (e.g., Smith et al. 2019*a*), additional caution is warranted for treating sagebrush in any area that may be used by sage-grouse outside of the breeding season.

MANAGEMENT IMPLICATIONS

Our findings support a body of evidence that sage-grouse inhabiting Wyoming big sagebrush do not respond positively to sagebrush reduction treatments. Because invertebrates and vegetation did not respond positively to Wyoming big sagebrush reduction, treatments provided little benefit for sage-grouse populations during any stage of their life cycle. Rather, the reduction of sagebrush cover resulting from treatments can adversely affect sage-grouse and other sagebrush-obligate species that nest within or beneath sagebrush shrubs and use shrubs as refugia from predators. Our results, however, are not comparable to mountain big sagebrush communities, which respond differently to treatments compared with Wyoming big sagebrush. If treatments are deemed appropriate for the benefit of other species, such as wild ungulates or livestock, the avoidance of important sage-grouse nesting, brood-rearing, and winter habitat will help ensure that adequate sagebrush cover and height are retained within the landscape. Nonetheless, benefits of treating Wyoming big sagebrush for other species has not been documented. Rather than implementing vegetation treatments of questionable value to sage-grouse, management programs that focus on the maintenance of large, undisturbed tracts of sagebrush will best facilitate the persistence of sage-grouse populations and other species reliant on the sagebrush steppe.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All sage-grouse were captured, radio-marked, and monitored following approved University of Wyoming Institutional Animal Care and Use Committee protocols (03132011, 20140128JB0059, and 20170322JL00266) and WGFD Chapter 33 scientific research permit 801.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A: WYOMING BIG SAGEBRUSH TREATMENT STUDY DESIGN

We employed a use-availability design to evaluate early brood-rearing sage-grouse habitat selection (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We identified resource use as locations obtained from relocations of radio-marked sage-grouse during 2011 and 2012 and pooled locations across individuals to represent a population-level response (Type 1 design; Manly et al. 2002, Thomas and Taylor 2006). We generated 5 times the number of use locations across the study area to represent available habitat. Available locations were randomly located across a 100% minimum convex polygon generated from sage-grouse use locations during the early brood-rearing period (first 2 weeks following nest hatch; Thompson et al. 2006). We used data from the Northwest Gap Analysis Program (2009) to constrain random locations to potential habitat by excluding areas that were inappropriate to be considered as available habitat such as exposed rock, open water, and stands of conifer. We down weighted available units to account for overrepresentation bias (Aldridge and Boyce 2007, Carpenter et al. 2010).

We considered a suite of predictor variables on the basis of *a priori* information from previous landscape-scale research on sage-grouse habitat (Homer et al. 1993, Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010, Doherty et al. 2010, Kirol et al. 2015; Table A1). These variables encompassed environmental categories that were evaluated at 3 spatial scales around used and available points: 0.28-km radii (0.25 km^2), 0.56-km radii (1.00 km^2), and 1.26-km radii (4.99 km^2). Spatial scales were based on previous research documenting relationships between landscape features and sage-grouse selection at those scales (Berry and Eng 1985, Holloran and Anderson 2005, Aldridge and Boyce 2007, Doherty et al. 2010).

We used remotely sensed sagebrush products (Homer et al. 2012; Table A1), to estimate percentage canopy cover of sagebrush (all species combined), big sagebrush (all subspecies combined), Wyoming big sagebrush, shrubs (all species), herbaceous cover, bare ground, and litter. We calculated the mean estimated percent cover and the standard deviation for each variable across the 3 spatial scales. We used standard deviation as a proxy for habitat diversity or heterogeneity (Kastdalen et al. 2003, Carpenter et al. 2010). We assessed quadratic relationships to evaluate potential nonlinear responses in mean percent cover estimates of all sagebrush and shrub categories (i.e.,

TABLE A1 Variables used in the model selection analysis evaluating greater sage-grouse early brood-rearing habitat selection in Fremont and Natrona counties, central Wyoming, USA, 2011 and 2012.

Variable names	Description
Bsage[a]	Mean big sagebrush cover (%; Homer et al. 2012)
Bsagesd	Standard deviation of big sagebrush cover (%; Homer et al. 2012)
DEM	Digital elevation model to calculate aspect, slope, and elevation (U.S. Geological Survey 2011)
NDVI	Normalized difference vegetation index (U.S. Department of Agriculture 2010)
Sage[a]	Mean sagebrush (all species) cover (%; Homer et al. 2012)
Sagesd	Standard deviation of sagebrush cover (%; Homer et al. 2012)
Shrub[a]	Mean shrub cover (%; Homer et al. 2012)
Shrubsd	Standard deviation of shrub cover (%; Homer et al. 2012)
Shrubhgt	Mean shrub height (cm; Homer et al. 2012)
Shrubhgtsd	Standard deviation of shrub height (cm; Homer et al. 2012)
VRM	Mean topographic roughness (vector roughness measure [VRM]; Sappington et al. 2007)
Wysage[a]	Mean Wyoming big sagebrush cover (%; Homer et al. 2012)
Wysagesd	Standard deviation of Wyoming big sagebrush cover (%; Homer et al. 2012)

[a]Quadratic transformation assessed.

potential selection for intermediate landscape features; Dzialak et al. 2013). In addition, we calculated estimated mean and standard deviation of height for all shrub species (Homer et al. 2012).

We used a 10-m digital elevation map (U.S. Geological Survey 2011) to calculate slope, aspect, and elevation. We used these estimates to determine a vector ruggedness measure (VRM); VRM uses the variation in slope and aspect to create a single measure of terrain ruggedness (Sappington et al. 2007). We calculated VRM values using a 3 × 3 cell format (Sappington et al. 2007). We rescaled VRM values by multiplying the original values by 1,000 for ease of interpretation. In addition, we derived NDVI (measure of surface greenness) from National Agriculture Imagery Program (NAIP) color aerial imagery (U.S. Department of Agriculture 2010).

Statistical methods

We computed a Pearson's correlation matrix to test for multicollinearity among predictor variables and omitted 1 of each correlated variable when coefficients were correlated ($|r| \geq 0.7$). We inspected tolerance (t) values and removed 1 of the correlated variables when $|t| \leq 0.40$ (Allison 2009, SAS Institute 2011). We checked for stability and consistency of regression coefficient estimates when variables were moderately correlated ($0.3 \leq |r| \leq 0.7$). Undetected correlations between variables may cause instability in the signs of coefficients and result in inflated standard errors (Doherty 2008). If variables were correlated, we retained the variable with the lowest AIC score. We did not permit correlated variables to compete in the same model at any level of model selection.

We used AIC_c to assess model support (Burnham and Anderson 2002). For all scale-dependent variables, we examined the 3 spatial scales (described above) to determine the scale that was most correlated to sage-grouse early brood selection by testing each variable scale individually and comparing AIC_c scores (Arnold 2010, Carpenter et al. 2010, Doherty et al. 2010). For each variable, we retained the scale with the lowest AIC_c score corresponding to the greatest predictive potential (Burnham and Anderson 2002). After selection of the most appropriate scale, we removed unsupported variables based on whether 85% confidence intervals around odds ratios included 1 (Hosmer and Lemeshow 2000, Arnold 2010). An odds ratio of 1 indicates no significant difference between used and available habitat units (Hosmer and Lemeshow 2000). We used variable screening to remove unsupported predictor variables, thereby reducing the likelihood of overfitting models in our model selection process (Burnham and Anderson 2002, Arnold 2010).

We used a sequential model selection approach (Arnold 2010) by evaluating the relative importance of predictor variables for selection. We explored all variable combinations (Burnham and Anderson 2002). We considered models with AIC_c scores in the range of 0–7 units (Burnham and Anderson 2002) to be competitive with the top model. We assessed variable importance by summing Akaike model weights across models that included the variable of interest (Arnold 2010). When a single top model was not apparent based on AIC_c scores (≤7 units considered competitive) we used multi-model inference to calculate final parameter coefficients, 95% confidence intervals, and odds ratios. We determined confidence sets for those models where Akaike weights (w_i) were within 10% of the top model (Burnham and Anderson 2002). At the final level of model selection, we further filtered variables with poor support for a true statistical difference between groups that had odds ratios with 95% confidence intervals that overlapped 1 (Hosmer and Lemeshow 2000). We performed a 5-fold cross validation to evaluate the predictive performance of our top model (Boyce et al. 2002). We conducted all statistical analyses with Statistical Analysis Software (SAS), version 9.3 (SAS Institute 2011).

We mapped our final resource selection model with 30-m pixel resolution across the study area. For interpretation, we mapped the final RSF with values rescaled between 0 and 1 (linear stretch; DeCesare et al. 2012) where 1 represented the highest and 0 the lowest predicted relative probability of selection. We distributed our predicted probabilities into 4 quartiles on the basis of percentile breaks in predicted probabilities (Sawyer et al. 2006). We assigned areas of high relative probability of selection (highest 25% of predicted probabilities for summer resource selection) a value of 4, moderate-high (51–75% predicted probabilities for summer resource selection) a value of 3, moderate-low (26–50% predicted probabilities for summer resource selection) a value of 2, and low (lowest 25% of predicted probabilities for summer resource selection) a value of 1.

Results

Seventeen models, which included 6 predictor variables at 2 spatial scales, made up our candidate set for early brood-rearing habitat selection. At the 0.25-km^2 (0.28-km radius) scale, shrub height was negatively correlated with selection and shrub cover was positively correlated with selection. Shrub cover and NDVI were positive predictors of selection when averaged across 4.99 km^2 (1.26-km radius). In contrast, variability (as measured by standard deviation) in Wyoming big sagebrush was a strong negative predictor of selection at the 4.99-km^2 scale. Because our candidate set contained more than 1 model, we performed model averaging to estimate parameter coefficients, 95% confidence intervals, and odds ratios for all variables contained within the candidate set.

Model averaging indicated that the 95% confidence interval for the odds ratios of distance to water, shrub height, and variability of shrub height overlapped 1 and were therefore considered uninformative predictors of habitat selection. Our best approximating model of sage-grouse early brood-rearing habitat consisted of shrub cover (0.28-km radius), NDVI (1.260-km radius), and variability in Wyoming big sagebrush cover (1.26-km radius; Table A2). Cross-validation indicated that our best model was a strong positive predictor of sage-grouse early brood-rearing habitat use ($r_s = 0.96$, $P = 0.001$, $n = 10$).

Through the process of developing an RSF and retaining the 2 highest predicted relative probability bins, we overlaid clusters of early brood-rearing locations that were spatially separated across our study area and located 6 spatially distinct project treatment locations (2 mowing, 2 tebuthiuron, and 2 off-site control sites). This was attributed to the spatial arrangement of leks that we chose for capture, because females occupied habitats in the relative vicinity of the lek in which they were bred, but also the habitat conditions present in those locations that were being used. Because of the relatively high site fidelity of sage-grouse across years (Berry and Eng 1985, Dunn and Braun 1985, Fischer et al. 1993, Holloran and Anderson 2005), we deemed that clusters of sage-grouse use locations during the early brood-rearing period were appropriate for outlining treatment areas. This ensured that 1) locations were in suitable sage-grouse habitat in a location that we could test for a response to sagebrush treatments, and 2) grouse have occurred in and likely will occur in these locations in the future. We buffered each location by the mean distance between the nest and the week 2 early brood-rearing locations (1,048 m; K. T. Smith, unpublished data). We then generated a 100% minimum convex polygon around buffered locations that were within similar clusters of use locations.

We restricted potential treatment areas to locations falling in the 2 highest predicted probability bins. We removed from consideration locations of cultural significance, such as historical trails, and locations where long-term rangeland monitoring takes place (BLM Lander Field Office, personal communication). Following WGFD

TABLE A2 Parameter estimates, variable importance values, and odds ratios for variables that were included in top models depicting greater sage-grouse early brood-rearing habitat selection in Fremont and Natrona counties, central Wyoming, USA, 2011 and 2012.

Parameter[a,b]	Estimate	95% CI		Variable importance	Odds ratio	95% CI	
		Lower	Upper			Lower	Upper
Intercept	−4.26	−6.99	−1.53				
$NDVI_{1260}$	0.03	0.02	0.03	0.92	1.02	1.01	1.03
$Shrub_{283}$	0.10	0.013	0.18	0.70	1.10	1.01	1.20
$Wysagesd_{1260}$	−0.49	−0.86	−0.13	0.82	0.61	0.43	0.88

[a]Parameters include normalized difference vegetation index (NDVI), shrub cover (Shrub), and standard deviation of Wyoming big sagebrush cover (Wysagesd).

[b]Subscripts for predictor variables correspond to the 3 circular analysis regions: 0.28-km radii (283), 0.564-km radii (564), and 1.26-km radii (1260).

protocols (WGFD 2011), we buffered known leks within the study area by 0.97 km (2.96 km^2) and removed locations closer than 0.97 km to leks from treatment consideration.

We followed the State of Wyoming Executive Order 2011-5 guidelines detailing sage-grouse Core Area protection to calculate the maximum allowable disturbance by means of the DDCT for our proposed project areas (State of Wyoming 2011). Stipulations for the DDCT were found in the WGFD protocols for treating sagebrush (WGFD 2011). We digitized existing disturbance using NAIP imagery (U.S. Department of Agriculture 2010). Disturbance included any human alterations such as roads, energy infrastructure, and human dwellings. We used geographic information predictor variables from our best approximating models to further refine suitable treatment locations within overall project locations. We removed locations when shrub cover was less than 2 standard deviations of the mean shrub cover at grouse use locations (7.9% as computed from Homer et al. [2012] shrub layer) so we would not treat locations containing sparse shrub cover. We considered treatment locations as suitable if they were in areas >100 m from water, with <15% slope, and that had VRM values <2 standard deviations above the mean VRM for grouse use locations. Removing steep slopes and high ruggedness (VRM) was a precautionary measure to ensure accessibility and equipment operator safety during treatment. Within the 4 treatment areas, we generated *n* = 4–5 2.59-km^2 polygons that we used to demarcate locations for treatment in each of the 4 treatment sites.

We treated sagebrush (Spike® 20P [active ingredient, tebuthiuron] and mechanical mowing) in early brood-rearing habitat during winter and spring 2014. We used female early brood-rearing locations and areas that were predicted to have high early brood-rearing occurrence to identify 4 treatment locations (2 Spike® 20P and 2 mowing treatments) and 2 off-site control locations, as described above. Treatments followed WGFD protocols (WGFD 2011). During January and February 2014, the WGFD and the University of Wyoming mowed approximately 489 ha of sagebrush across 2 mowing treatment areas. Spike® 20P application occurred in early May 2014. We contracted with Ag Flyers, Inc. of Torrington, Wyoming to apply 1.12 kg/ha (0.22 kg/ha active ingredient), anticipating a 50% kill rate of sagebrush, to 6.1 km^2 across 2 study areas.

APPENDIX B: MEASURED VEGETATION CHARACTERISTICS

(See Tables B1–B6).

TABLE B1 Mean habitat characteristics (SE) in each mowing treatment study area and adjacent untreated control sites during 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA.

Parameter	2014	2015	2016	2017	2018	2019
Mowing treatment area A						
Live big sagebrush canopy cover (%)	7.59 (0.97)	6.88 (1.24)	9.26 (1.47)	8.19 (1.37)	8.47 (1.72)	8.63 (1.74)
Dead big sagebrush canopy cover (%)	3.09 (0.46)	2.44 (0.45)	2.47 (0.53)	3.27 (0.55)	1.40 (0.34)	2.52 (0.60)
Big sagebrush height (cm)	15.46 (0.58)	14.60 (0.71)	15.87 (0.66)	13.87 (0.47)	17.23 (0.94)	16.31 (0.60)
Perennial grass cover (%)	19.32 (1.16)	18.31 (0.85)	22.31 (1.25)	22.09 (1.31)	14.25 (0.69)	14.65 (0.84)
Perennial grass height (cm)	33.71 (1.04)	30.62 (0.82)	23.98 (1.15)	34.00 (1.48)	26.18 (1.34)	20.97 (0.85)
Forb cover (%)	6.41 (1.06)	8.01 (0.88)	7.47 (1.10)	8.32 (1.11)	4.52 (0.85)	4.93 (0.91)
Forb species richness	1.21 (0.15)	1.15 (0.13)	1.49 (0.13)	1.29 (0.14)	0.88 (0.14)	1.52 (0.17)
Adjacent control area A						
Live big sagebrush canopy cover (%)	14.22 (1.72)	14.40 (2.53)	17.17 (1.83)	17.20 (1.99)	19.02 (2.18)	15.75 (2.13)

TABLE B1 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Dead big sagebrush canopy cover (%)	1.16 (0.26)	1.17 (0.23)	0.92 (0.19)	1.90 (0.51)	0.58 (0.20)	1.65 (0.42)
Big sagebrush height (cm)	28.23 (2.70)	26.77 (2.33)	27.76 (2.71)	27.51 (3.22)	29.35 (2.16)	26.56 (2.51)
Perennial grass cover (%)	19.33 (1.82)	16.46 (0.69)	19.18 (1.03)	18.67 (1.09)	15.65 (1.13)	12.99 (1.14)
Perennial grass height (cm)	35.35 (1.54)	27.99 (1.02)	23.04 (0.91)	33.89 (1.07)	28.96 (0.88)	21.32 (0.72)
Forb cover (%)	6.78 (2.15)	11.38 (1.38)	11.31 (1.57)	13.48 (1.58)	8.87 (1.09)	6.35 (0.98)
Forb species richness	1.28 (0.21)	1.66 (0.27)	1.78 (0.20)	1.81 (0.14)	1.50 (0.26)	1.54 (0.26)
Mowing treatment area B						
Live big sagebrush canopy cover (%)	8.07 (1.73)	8.75 (2.48)	10.19 (1.73)	11.27 (2.55)	10.52 (1.38)	11.35 (1.94)
Dead big sagebrush canopy cover (%)	3.87 (0.49)	4.83 (0.43)	4.64 (0.69)	5.54 (0.80)	2.34 (0.40)	3.56 (0.18)
Big sagebrush height (cm)	15.50 (0.47)	14.67 (0.89)	17.20 (0.62)	15.35 (0.72)	17.57 (0.53)	17.74 (0.62)
Perennial grass cover (%)	19.17 (2.18)	17.06 (2.12)	17.90 (1.43)	20.97 (2.25)	11.08 (0.88)	14.85 (1.26)
Perennial grass height (cm)	27.70 (0.97)	28.65 (1.96)	20.96 (0.64)	29.58 (1.05)	21.66 (0.57)	20.87 (0.72)
Forb cover (%)	4.72 (1.35)	4.90 (0.94)	7.76 (2.72)	9.16 (2.01)	3.86 (0.92)	7.37 (1.24)
Forb species richness	1.11 (0.21)	0.84 (0.14)	1.18 (0.20)	1.06 (0.15)	0.78 (0.19)	1.71 (0.12)
Adjacent control area B						
Live big sagebrush canopy cover (%)	17.27 (2.19)	17.64 (1.80)	19.90 (2.57)	19.81 (2.24)	18.32 (2.28)	19.77 (2.15)
Dead big sagebrush canopy cover (%)	0.85 (0.31)	1.24 (0.51)	1.39 (0.55)	2.51 (0.63)	1.47 (0.45)	1.27 (0.37)
Big sagebrush height (cm)	27.18 (2.16)	27.64 (3.09)	28.88 (2.71)	27.14 (2.11)	26.91 (2.00)	28.59 (2.24)
Perennial grass cover (%)	17.13 (2.04)	13.11 (0.79)	15.86 (1.01)	16.53 (1.84)	12.25 (1.14)	11.28 (1.08)
Perennial grass height (cm)	28.78 (1.37)	26.39 (1.01)	21.50 (0.93)	31.74 (0.94)	23.78 (1.22)	20.38 (1.03)
Forb cover (%)	5.70 (1.45)	4.28 (0.72)	6.61 (1.46)	11.86 (1.18)	4.77 (1.10)	7.11 (0.92)
Forb species richness	0.84 (0.12)	0.62 (0.16)	1.34 (0.15)	1.08 (0.10)	0.78 (0.14)	1.35 (0.16)

TABLE B2 Mean habitat characteristics (SE) in each tebuthiuron treatment study area and adjacent untreated control sites during 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA.

Parameter	2014	2015	2016	2017	2018	2019
Tebuthiuron treatment area A						
Live big sagebrush canopy cover (%)	22.06 (1.83)	10.90 (1.43)	13.88 (1.83)	8.53 (1.41)	11.91 (1.30)	10.71 (1.62)
Dead big sagebrush canopy cover (%)	1.75 (0.59)	12.31 (1.22)	10.40 (0.85)	14.23 (1.22)	7.05 (0.69)	8.45 (0.96)

(Continues)

TABLE B2 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Big sagebrush height (cm)	23.70 (2.29)	19.24 (1.57)	23.06 (2.05)	22.54 (2.53)	26.91 (2.85)	24.90 (2.47)
Perennial grass cover (%)	14.43 (2.24)	17.18 (0.93)	22.94 (1.67)	20.59 (1.69)	15.74 (0.69)	17.65 (1.63)
Perennial grass height (cm)	30.76 (1.31)	31.97 (1.45)	27.85 (1.76)	38.25 (1.96)	26.92 (1.25)	22.24 (1.33)
Forb cover (%)	4.11 (1.15)	11.46 (1.87)	6.05 (1.22)	6.20 (0.98)	4.67 (1.31)	5.21 (1.24)
Forb species richness	0.92 (0.26)	0.99 (0.24)	0.89 (0.18)	0.94 (0.15)	0.66 (0.17)	1.05 (0.22)
Adjacent control area A						
Live big sagebrush canopy cover (%)	23.66 (3.51)	17.96 (3.12)	20.69 (2.74)	17.48 (3.06)	18.67 (3.63)	17.51 (3.93)
Dead big sagebrush canopy cover (%)	3.51 (2.67)	3.12 (5.94)	2.74 (4.84)	3.06 (6.95)	3.63 (3.22)	3.93 (4.59)
Big sagebrush height (cm)	27.62 (3.31)	22.86 (3.02)	25.49 (3.44)	25.30 (4.24)	27.79 (4.51)	28.02 (3.93)
Perennial grass cover (%)	8.64 (1.44)	15.79 (0.83)	17.18 (1.92)	17.36 (1.64)	14.39 (1.58)	13.16 (1.91)
Perennial grass height (cm)	30.47 (0.84)	30.45 (0.85)	24.95 (1.64)	32.96 (1.54)	25.41 (1.84)	22.82 (0.83)
Forb cover (%)	7.59 (1.77)	10.12 (1.94)	6.56 (1.17)	9.69 (1.58)	5.01 (1.34)	4.76 (0.83)
Forb species richness	1.04 (0.19)	0.97 (0.18)	0.97 (0.07)	0.94 (0.11)	0.74 (0.14)	0.92 (0.14)
Tebuthiuron treatment area B						
Live big sagebrush canopy cover (%)	22.87 (1.88)	11.03 (0.97)	11.94 (1.51)	12.55 (1.59)	14.21 (1.58)	16.75 (1.65)
Dead big sagebrush canopy cover (%)	1.05 (0.28)	11.80 (1.45)	10.43 (1.38)	8.19 (1.28)	5.51 (0.79)	5.04 (0.50)
Big sagebrush height (cm)	31.09 (1.75)	25.22 (1.44)	30.99 (1.45)	29.69 (1.57)	32.64 (1.85)	32.57 (1.94)
Perennial grass cover (%)	20.93 (2.77)	17.12 (1.20)	13.19 (1.22)	25.84 (2.60)	12.84 (0.74)	18.47 (2.49)
Perennial grass height (cm)	40.56 (1.15)	26.79 (0.99)	21.08 (0.89)	39.02 (1.08)	28.75 (1.23)	21.32 (1.13)
Forb cover (%)	8.49 (1.22)	15.12 (1.17)	13.76 (1.37)	12.97 (2.02)	12.39 (2.67)	13.97 (2.00)
Forb species richness	1.55 (0.23)	2.36 (0.26)	2.22 (0.23)	1.68 (0.18)	1.70 (0.15)	2.14 (0.18)
Adjacent control area B						
Live big sagebrush canopy cover (%)	11.09 (2.15)	9.99 (1.68)	9.39 (1.55)	11.12 (1.36)	12.37 (1.59)	14.38 (1.87)
Dead big sagebrush canopy cover (%)	1.20 (0.72)	2.80 (1.50)	3.21 (1.11)	2.51 (0.95)	1.47 (0.73)	1.69 (0.65)
Big sagebrush height (cm)	26.15 (1.79)	23.17 (1.26)	27.36 (1.75)	26.29 (1.64)	28.95 (1.21)	27.19 (1.14)
Perennial grass cover (%)	19.68 (1.97)	16.51 (0.98)	14.08 (1.20)	26.34 (1.53)	11.40 (1.14)	15.10 (1.27)
Perennial grass height (cm)	40.32 (1.12)	26.84 (1.18)	19.48 (0.45)	35.97 (0.96)	25.64 (0.86)	20.61 (0.90)
Forb cover (%)	6.10 (0.74)	11.92 (1.10)	11.47 (1.71)	7.03 (0.97)	7.78 (1.66)	11.91 (1.29)
Forb species richness	1.49 (0.15)	1.99 (0.19)	1.82 (0.11)	1.42 (0.16)	1.83 (0.18)	2.12 (0.22)

TABLE B3 Mean habitat characteristics (SE) in treated and untreated portions of temporary exclosures within mowing treatment study areas during 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA. We removed exclosure fencing in spring 2016.

Parameter	2014	2015	2016	2017	2018	2019
Temporary exclosures: Site A (treated)						
Live big sagebrush canopy cover (%)	11.17 (1.38)	7.91 (2.56)	12.04 (0.60)	7.51 (0.91)	8.66 (0.68)	10.17 (2.17)
Dead big sagebrush canopy cover (%)	1.44 (0.44)	3.09 (2.32)	3.84 (0.97)	2.67 (0.63)	2.13 (1.06)	3.17 (0.86)
Big sagebrush height (cm)	17.67 (1.19)	19.26 (1.75)	18.74 (0.41)	17.22 (0.97)	21.89 (0.66)	19.15 (1.17)
Perennial grass cover (%)	25.16 (6.72)	16.86 (0.93)	23.14 (2.12)	23.82 (3.59)	17.35 (0.95)	17.60 (3.36)
Perennial grass height (cm)	29.02 (1.75)	36.27 (1.41)	22.12 (0.12)	30.69 (1.05)	26.45 (1.14)	21.61 (2.36)
Forb cover (%)	4.65 (2.27)	6.35 (2.70)	8.43 (0.77)	6.50 (0.16)	5.81 (1.24)	5.30 (1.51)
Forb species richness	0.82 (0.33)	0.98 (0.28)	1.02 (0.14)	1.24 (0.14)	0.67 (0.13)	1.20 (0.40)
Temporary exclosures: Site A (untreated)						
Live big sagebrush canopy cover (%)	14.72 (2.33)	13.56 (2.04)	17.16 (1.69)	16.08 (2.82)	17.86 (0.46)	21.61 (1.17)
Dead big sagebrush canopy cover (%)	0.45 (0.24)	1.46 (1.29)	1.63 (0.50)	1.27 (0.48)	0.82 (0.32)	1.29 (0.38)
Big sagebrush height (cm)	27.05 (3.02)	23.71 (3.92)	30.12 (0.32)	27.04 (2.00)	28.09 (2.17)	30.14 (1.44)
Perennial grass cover (%)	16.47 (2.01)	19.07 (1.61)	16.57 (2.70)	20.44 (0.75)	13.43 (1.80)	17.70 (3.44)
Perennial grass height (cm)	31.33 (1.07)	33.43 (2.91)	26.02 (1.22)	32.10 (1.76)	28.47 (1.83)	22.55 (0.24)
Forb cover (%)	5.25 (2.81)	10.05 (3.28)	13.15 (1.73)	12.94 (1.72)	3.79 (1.36)	5.18 (1.78)
Forb species richness	1.08 (0.24)	0.71 (0.21)	1.61 (0.04)	1.51 (0.24)	1.14 (0.20)	1.65 (0.28)
Temporary exclosures: Site B (treated)						
Live big sagebrush canopy cover (%)	8.59 (2.44)	8.22 (2.26)	12.13 (0.16)	7.99 (0.76)	15.97 (3.58)	12.93 (2.48)
Dead big sagebrush canopy cover (%)	4.41 (1.67)	6.09 (1.30)	3.04 (0.39)	5.68 (1.26)	2.53 (0.51)	3.54 (0.66)
Big sagebrush height (cm)	16.70 (2.41)	17.49 (2.34)	19.02 (1.76)	16.42 (0.93)	20.20 (1.30)	19.67 (1.24)
Perennial grass cover (%)	26.87 (7.26)	18.64 (2.01)	26.19 (0.97)	19.85 (1.32)	13.74 (0.87)	17.35 (1.92)
Perennial grass height (cm)	24.06 (1.02)	38.84 (2.73)	20.33 (1.27)	29.41 (1.32)	20.47 (0.83)	23.10 (1.75)
Forb cover (%)	2.98 (0.53)	4.18 (2.81)	7.06 (2.47)	7.82 (0.50)	4.27 (2.60)	8.53 (2.93)
Forb species richness	1.04 (0.20)	0.90 (0.37)	0.96 (0.14)	0.86 (0.22)	1.04 (0.51)	2.22 (0.67)
Temporary exclosures: Site B (untreated)						
Live big sagebrush canopy cover (%)	17.47 (2.70)	16.33 (1.32)	23.13 (0.46)	18.71 (1.89)	22.34 (1.61)	19.10 (1.60)
Dead big sagebrush canopy cover (%)	0.53 (0.32)	0.88 (0.15)	1.07 (0.33)	1.64 (0.30)	0.34 (0.24)	1.13 (0.28)
Big sagebrush height (cm)	27.36 (1.57)	24.19 (2.68)	30.76 (2.66)	27.10 (2.76)	29.97 (3.68)	29.18 (3.36)

(Continues)

TABLE B3 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Perennial grass cover (%)	11.34 (3.68)	15.83 (0.83)	17.50 (1.12)	14.46 (0.85)	13.04 (0.65)	11.91 (1.85)
Perennial grass height (cm)	26.29 (1.03)	31.27 (1.21)	21.10 (1.01)	32.14 (0.89)	21.06 (2.36)	23.65 (2.60)
Forb cover (%)	1.38 (0.44)	11.64 (3.21)	8.63 (1.79)	17.36 (3.15)	4.94 (0.48)	7.59 (2.00)
Forb species richness	0.90 (0.21)	0.90 (0.30)	1.67 (0.42)	1.41 (0.33)	1.24 (0.53)	1.49 (0.48)

TABLE B4 Mean habitat characteristics (SE) in treated and untreated portions of temporary exclosures within tebuthiuron treatment study areas 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA. We removed exclosure fencing in spring 2016.

Parameter	2014	2015	2016	2017	2018	2019
Temporary exclosures: Site A (treated)						
Live big sagebrush canopy cover (%)	18.53 (2.38)	14.32 (5.47)	17.43 (6.16)	11.45 (4.30)	15.13 (6.23)	14.22 (6.81)
Dead big sagebrush canopy cover (%)	1.16 (0.58)	5.94 (1.57)	4.93 (1.01)	8.56 (1.93)	7.12 (2.77)	7.72 (2.69)
Big sagebrush height (cm)	21.91 (4.42)	23.72 (4.28)	23.17 (3.24)	21.88 (3.22)	22.28 (4.05)	21.99 (2.58)
Perennial grass cover (%)	9.84 (1.52)	13.06 (1.51)	11.07 (2.92)	14.72 (1.08)	15.96 (1.48)	13.76 (2.06)
Perennial grass height (cm)	22.67 (0.27)	31.27 (0.92)	28.14 (0.97)	32.37 (1.79)	30.12 (3.34)	22.04 (1.20)
Forb cover (%)	2.38 (0.23)	8.29 (4.14)	9.31 (2.41)	8.48 (1.12)	3.84 (1.90)	5.18 (1.52)
Forb species richness	0.69 (0.13)	0.49 (0.21)	0.80 (0.22)	0.94 (0.27)	0.67 (0.12)	1.08 (0.13)
Temporary exclosures: Site A (untreated)						
Live big sagebrush canopy cover (%)	22.76 (4.37)	19.60 (5.26)	24.52 (4.39)	24.88 (5.68)	23.71 (6.16)	21.16 (7.43)
Dead big sagebrush canopy cover (%)	1.41 (0.88)	2.92 (1.21)	3.70 (0.95)	4.32 (1.22)	2.11 (1.54)	6.12 (2.29)
Big sagebrush height (cm)	30.50 (3.18)	26.97 (1.55)	28.13 (1.75)	27.71 (2.12)	28.81 (3.20)	27.04 (3.11)
Perennial grass cover (%)	20.72 (4.63)	15.64 (0.38)	19.90 (5.18)	16.21 (3.07)	13.04 (2.43)	8.42 (0.74)
Perennial grass height (cm)	27.84 (2.24)	36.33 (2.48)	24.00 (4.02)	31.84 (2.43)	25.43 (0.04)	19.61 (0.94)
Forb cover (%)	16.06 (5.31)	10.54 (3.44)	10.75 (3.85)	11.80 (1.81)	6.24 (2.23)	7.13 (1.04)
Forb species richness	1.27 (0.58)	0.71 (0.27)	1.14 (0.39)	1.27 (0.24)	0.84 (0.19)	1.43 (0.17)
Temporary exclosures: Site B (treated)						
Live big sagebrush canopy cover (%)	27.59 (5.64)	19.63 (4.68)	21.54 (3.91)	22.79 (6.82)	26.52 (7.27)	30.20 (9.87)
Dead big sagebrush canopy cover (%)	1.04 (0.41)	9.15 (4.20)	6.01 (3.28)	7.88 (1.83)	4.38 (2.53)	3.67 (1.33)
Big sagebrush height (cm)	39.39 (5.29)	34.94 (5.34)	36.53 (3.38)	40.63 (6.40)	40.24 (4.92)	45.26 (8.84)
Perennial grass cover (%)	18.47 (5.32)	15.79 (0.40)	13.46 (2.10)	18.04 (2.25)	16.77 (2.74)	10.85 (3.45)

TABLE B4 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Perennial grass height (cm)	30.22 (1.61)	35.61 (0.72)	19.25 (1.02)	38.18 (4.30)	24.71 (2.75)	19.84 (0.90)
Forb cover (%)	13.86 (3.61)	15.30 (4.50)	15.94 (4.49)	11.25 (2.13)	16.97 (7.23)	14.70 (2.73)
Forb species richness	2.53 (0.44)	2.02 (0.41)	2.29 (0.19)	1.63 (0.21)	2.49 (0.24)	2.65 (0.31)
Temporary exclosures: Site B (untreated)						
Live big sagebrush canopy cover (%)	28.33 (8.48)	29.18 (5.52)	38.32 (2.49)	31.12 (7.86)	31.73 (9.08)	31.22 (6.24)
Dead big sagebrush canopy cover (%)	1.33 (1.08)	8.43 (4.16)	4.38 (0.59)	5.98 (2.15)	3.60 (1.38)	3.84 (2.41)
Big sagebrush height (cm)	38.39 (8.11)	35.60 (5.90)	41.03 (4.29)	37.63 (7.81)	40.21 (4.23)	45.31 (5.91)
Perennial grass cover (%)	31.82 (7.40)	14.90 (2.52)	15.94 (2.92)	14.07 (0.47)	11.41 (1.27)	12.40 (0.58)
Perennial grass height (cm)	30.61 (1.60)	24.80 (4.25)	18.94 (0.85)	36.75 (0.36)	24.16 (2.660)	19.33 (1.99)
Forb cover (%)	16.50 (2.15)	11.84 (2.23)	13.35 (2.62)	21.04 (4.77)	20.67 (0.73)	12.19 (0.88)
Forb species richness	1.73 (0.21)	1.06 (0.16)	2.00 (0.18)	2.12 (0.22)	2.71 (0.07)	2.12 (0.06)

TABLE B5 Mean habitat characteristics (SE) in treated and untreated portions of permanent exclosures within mowing treatment study areas during 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA.

Parameter	2014	2015	2016	2017	2018	2019
Permanent exclosures: Site A (treated)						
Live big sagebrush canopy cover (%)	3.87 (0.72)	7.75 (0.55)	7.27 (1.76)	5.17 (0.57)	9.09 (2.34)	7.09 (0.45)
Dead big sagebrush canopy cover (%)	4.39 (1.16)	5.41 (0.92)	5.44 (0.99)	7.70 (1.44)	4.47 (1.51)	6.41 (1.27)
Big sagebrush height (cm)	15.47 (0.81)	17.42 (1.51)	17.99 (1.70)	17.26 (1.45)	21.72 (1.31)	21.65 (1.28)
Perennial grass cover (%)	17.56 (0.56)	20.49 (1.24)	25.59 (2.76)	25.83 (5.59)	16.18 (0.85)	22.55 (2.76)
Perennial grass height (cm)	28.51 (0.99)	47.24 (4.30)	25.82 (1.77)	32.59 (3.40)	28.86 (1.35)	21.41 (1.10)
Forb cover (%)	7.09 (2.43)	8.25 (2.36)	11.84 (3.25)	10.07 (1.30)	6.10 (1.83)	7.71 (1.15)
Forb species richness	1.29 (0.10)	1.24 (0.51)	1.41 (0.27)	1.53 (0.22)	1.31 (0.46)	1.43 (0.19)
Permanent exclosures: Site A (untreated)						
Live big sagebrush canopy cover (%)	19.92 (1.89)	15.60 (2.19)	20.94 (2.31)	17.94 (0.62)	20.27 (2.64)	17.84 (2.50)
Dead big sagebrush canopy cover (%)	0.63 (0.25)	1.08 (0.23)	3.11 (0.74)	2.60 (1.33)	1.31 (0.49)	1.33 (0.45)
Big sagebrush height (cm)	29.32 (1.75)	28.29 (0.78)	30.61 (1.55)	27.18 (1.95)	32.38 (2.80)	30.59 (2.58)
Perennial grass cover (%)	29.47 (1.08)	16.03 (1.03)	17.75 (4.66)	24.51 (2.91)	14.56 (2.47)	13.87 (3.32)
Perennial grass height (cm)	31.63 (2.51)	37.20 (1.94)	25.96 (0.57)	33.59 (1.62)	27.71 (1.34)	22.86 (1.51)

(Continues)

TABLE B5 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Forb cover (%)	10.19 (6.31)	14.95 (3.15)	11.55 (5.43)	17.76 (3.77)	15.20 (10.06)	7.88 (2.05)
Forb species richness	1.27 (0.46)	1.39 (0.34)	1.61 (0.26)	2.12 (0.34)	1.27 (0.60)	1.16 (0.11)
Permanent exclosures: Site B (treated)						
Live big sagebrush canopy cover (%)	3.87 (0.72)	7.75 (0.55)	7.27 (1.76)	5.17 (0.57)	9.09 (2.34)	7.09 (0.45)
Dead big sagebrush canopy cover (%)	4.39 (1.16)	5.41 (0.92)	5.44 (0.99)	7.70 (1.44)	4.47 (1.51)	6.41 (1.27)
Big sagebrush height (cm)	15.47 (0.81)	17.42 (1.51)	17.99 (1.70)	17.26 (1.45)	21.72 (1.31)	21.65 (1.28)
Perennial grass cover (%)	17.56 (0.56)	20.49 (1.24)	25.59 (2.76)	25.83 (5.59)	16.18 (0.85)	22.55 (2.76)
Perennial grass height (cm)	28.51 (0.99)	47.24 (4.30)	25.82 (1.77)	32.59 (3.40)	28.86 (1.35)	21.41 (1.10)
Forb cover (%)	7.09 (2.43)	8.25 (2.36)	11.84 (3.25)	10.07 (1.30)	6.10 (1.83)	7.71 (1.15)
Forb species richness	1.29 (0.10)	1.24 (0.51)	1.41 (0.27)	1.53 (0.22)	1.31 (0.46)	1.43 (0.19)
Permanent exclosures: Site B (untreated)						
Live big sagebrush canopy cover (%)	16.76 (2.97)	16.50 (1.31)	22.16 (1.83)	18.89 (1.97)	21.09 (2.02)	21.48 (2.80)
Dead big sagebrush canopy cover (%)	1.29 (0.76)	2.67 (0.88)	1.16 (0.22)	3.37 (0.77)	0.62 (0.23)	3.31 (1.43)
Big sagebrush height (cm)	22.11 (3.34)	22.41 (4.06)	26.17 (3.19)	21.66 (2.98)	24.47 (1.55)	23.56 (2.16)
Perennial grass cover (%)	22.68 (1.77)	16.49 (1.43)	23.63 (2.38)	17.30 (2.16)	13.69 (1.71)	16.37 (1.36)
Perennial grass height (cm)	24.04 (0.61)	37.08 (3.53)	25.24 (2.12)	29.71 (0.82)	25.35 (4.12)	24.06 (2.03)
Forb cover (%)	1.54 (0.56)	8.63 (4.48)	6.88 (1.12)	16.66 (2.29)	5.71 (2.71)	10.26 (0.44)
Forb species richness	0.63 (0.02)	0.71 (0.26)	1.53 (0.12)	1.25 (0.24)	1.33 (0.54)	1.86 (0.07)

TABLE B6 Mean habitat characteristics (SE) in treated and untreated portions of permanent exclosures within tebuthiuron treatment study areas during 2014–2019 field seasons in Fremont and Natrona counties, central Wyoming, USA.

Parameter	2014	2015	2016	2017	2018	2019
Permanent exclosures: Site A (treated)						
Live big sagebrush canopy cover (%)	17.16 (6.01)	16.04 (7.33)	17.16 (4.69)	12.33 (5.50)	13.86 (5.52)	16.78 (6.41)
Dead big sagebrush canopy cover (%)	0.53 (0.20)	11.44 (3.00)	12.17 (2.84)	11.26 (3.55)	7.76 (1.60)	6.86 (2.09)
Big sagebrush height (cm)	26.65 (7.74)	29.69 (13.14)	27.66 (7.86)	33.37 (10.19)	32.23 (8.27)	30.44 (7.92)
Perennial grass cover (%)	13.91 (4.00)	15.89 (1.46)	15.79 (3.05)	21.18 (4.88)	18.63 (3.44)	21.76 (4.29)
Perennial grass height (cm)	26.57 (0.87)	33.12 (2.36)	25.45 (1.54)	36.65 (2.10)	31.65 (2.82)	27.90 (2.16)

TABLE B6 (Continued)

Parameter	2014	2015	2016	2017	2018	2019
Forb cover (%)	5.99 (2.40)	7.86 (2.63)	6.40 (1.70)	5.90 (1.99)	7.47 (2.63)	4.98 (1.21)
Forb species richness	1.06 (0.32)	0.49 (0.17)	1.22 (0.57)	0.71 (0.16)	0.78 (0.19)	1.18 (0.39)
Permanent exclosures: Site A (untreated)						
Live big sagebrush canopy cover (%)	26.14 (9.82)	26.26 (8.65)	35.27 (8.66)	34.71 (6.82)	36.74 (7.56)	37.64 (10.08)
Dead big sagebrush canopy cover (%)	0.43 (0.42)	1.83 (0.60)	4.18 (1.10)	3.22 (0.69)	2.96 (0.76)	4.93 (0.40)
Big sagebrush height (cm)	38.82 (12.65)	37.17 (11.74)	41.59 (12.76)	38.18 (11.15)	37.86 (11.93)	40.43 (12.57)
Perennial grass cover (%)	21.45 (3.08)	19.12 (2.12)	26.57 (3.14)	20.69 (3.95)	21.82 (5.05)	16.44 (2.97)
Perennial grass height (cm)	25.55 (2.18)	39.18 (2.72)	29.08 (2.81)	32.41 (2.53)	29.04 (1.72)	24.61 (2.66)
Forb cover (%)	9.32 (4.47)	9.02 (1.74)	9.90 (2.19)	11.01 (2.12)	9.49 (0.97)	8.52 (2.88)
Forb species richness	0.96 (0.28)	0.61 (0.10)	0.96 (0.27)	1.25 (0.09)	1.14 (0.27)	1.39 (0.37)
Permanent exclosures: Site B (treated)						
Live big sagebrush canopy cover (%)	19.09 (1.41)	11.83 (2.54)	14.04 (1.39)	15.83 (4.82)	23.31 (4.47)	18.80 (3.44)
Dead big sagebrush canopy cover (%)	1.94 (0.92)	6.09 (1.91)	4.51 (1.28)	9.17 (2.40)	3.31 (0.76)	3.51 (1.29)
Big sagebrush height (cm)	28.27 (1.77)	25.96 (1.98)	28.07 (1.22)	27.52 (2.14)	30.59 (2.86)	30.44 (2.23)
Perennial grass cover (%)	25.44 (6.37)	15.88 (0.88)	22.79 (1.64)	21.13 (2.59)	20.94 (5.22)	18.43 (3.03)
Perennial grass height (cm)	32.35 (2.53)	36.22 (2.84)	26.96 (1.27)	37.57 (1.93)	33.00 (2.99)	27.29 (1.66)
Forb cover (%)	9.06 (2.19)	11.82 (1.71)	12.58 (1.66)	13.94 (1.53)	11.54 (2.53)	8.46 (1.19)
Forb species richness	1.67 (0.29)	1.76 (0.51)	2.43 (0.05)	1.37 (0.19)	2.16 (0.53)	2.39 (0.28)
Permanent exclosures: Site B (untreated)						
Live big sagebrush canopy cover (%)	20.00 (1.61)	18.36 (2.30)	24.37 (3.06)	25.28 (4.53)	27.53 (5.81)	23.79 (4.58)
Dead big sagebrush canopy cover (%)	0.74 (0.29)	4.98 (1.88)	1.24 (0.52)	2.46 (0.25)	1.38 (0.62)	2.39 (1.11)
Big height (cm)	32.22 (0.78)	25.94 (1.42)	29.97 (0.86)	27.20 (1.54)	31.50 (1.08)	30.66 (0.51)
Perennial grass cover (%)	22.36 (1.85)	19.41 (2.10)	30.74 (3.72)	20.01 (1.02)	14.37 (1.60)	12.75 (0.78)
Perennial grass height (cm)	29.66 (2.58)	24.12 (0.82)	25.45 (1.04)	37.67 (1.22)	29.22 (0.70)	22.80 (2.09)
Forb cover (%)	7.65 (0.60)	6.63 (2.62)	14.88 (3.44)	10.64 (2.27)	10.19 (2.58)	8.02 (1.73)
Forb species richness	1.75 (0.09)	0.80 (0.14)	2.12 (0.32)	1.51 (0.33)	2.06 (0.31)	1.80 (0.44)