FINAL RESEARCH REPORT

GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) NESTING AND EARLY BROOD-REARING HABITAT RESPONSE TO MOWING AND PRESCRIBED BURNING WYOMING BIG SAGEBRUSH AND INFLUENCE OF DISTURBANCE FACTORS ON LEK PERSISTENCE IN THE BIGHORN BASIN, WYOMING

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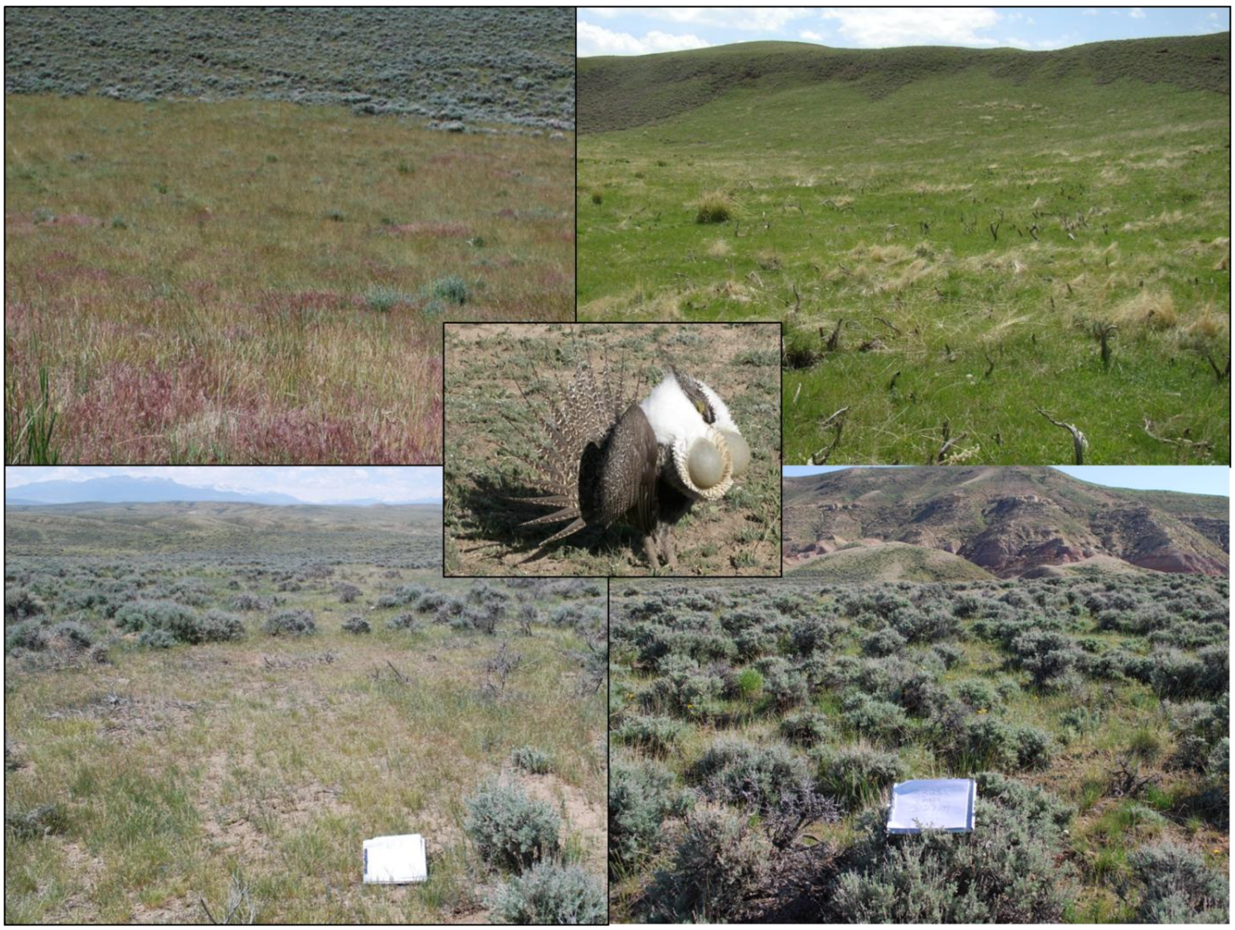

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SUMMARY

Our research focused on evaluating the relative influence of prescribed burning (1990–1999 and 2000–2006) and mowing (2000–2006) treatments on the quality of greater sage-grouse (*Centrocercus urophasianus*) nesting and early brood-rearing habitats and landscape characteristics that influenced sage-grouse lek persistence from 1980 to 2009 in the Bighorn Basin of north-central Wyoming. Objectives of treatments have focused on land health, watershed improvement, and to enhance habitat conditions for livestock, greater sage-grouse (*Centrocercus urophasianus*), and other wildlife. We focused on how prescribed burning and mowing may affect sage-grouse nesting and early brood-rearing habitats by evaluating habitat quality through insect, soil, and vegetation parameters at 30 treated sites compared to 30 nearby, untreated reference sites. Our sites were classified by treatment type, soil type, season, and decade of treatment (sites burned in the 1990s and sites burned or mowed during 2000–2006). Prescribed burning greatly (–85.1 to –100%) reduced levels of sagebrush canopy cover at least 19 years postburn, while mowing maintained minimum levels of sagebrush canopy cover recommended for sage-grouse nesting and early brood-rearing habitats. In some cases, prescribed burning showed positive results for sage-grouse nesting and early brood-rearing habitats compared to mowing such as 6.3- to 16.9-times greater ant weights (mg/trap; on aridic burns during 1990s and ustic burns during 2000–2006 respectively), 2.3- to 85.1-times greater beetle weights (mg/trap) on ustic soils, 3.6- to 4.3-times higher perennial grass canopy cover on aridic soils, 2.6-times higher plant species richness on aridic soils during 2000–2006 burns, and 2.0- to 5.0-times higher soil nitrogen on burns during 2000–2006, but all of these characteristics were not found to be enhanced compared to reference sites. Mowing provided 3.6- to 13.2-times higher sagebrush canopy cover on ustic soils, 2.2- to 3.0-times higher sagebrush heights on aridic

and ustic soils, and 1.2- to 1.5-times higher insect diversity on ustic and aridic soils than prescribed burning. When comparing mowed sites to reference sites, there was1.2- to 2.5-times higher litter and 3.5- to 9.1-times higher ant weights (mg/trap) at mowed sites. However, mowing did not promote an increase in other sage-grouse early brood-rearing needs such as the abundance of food forbs, abundance or weights of beetles and grasshoppers, or perennial grass canopy cover or height. Forb nutritional content and production were not enhanced (i.e., similar to reference sites) by either treatment. Perennial grass height and canopy cover (5 of 6 cases) were not enhanced through burning or mowing. The main benefit from prescribed burning was an increase in grasshopper abundance (no./trap) compared to reference sites (grasshopper abundance was 2.4- to 3.4-times greater at prescribed burned sites than reference sites). In general, results indicate few positive aspects of treating Wyoming big sagebrush to enhance habitat conditions for nesting and early brood-rearing sage-grouse as much as 19 years after prescribed burning and 9 years after mowing in the Bighorn Basin. Mowing, however, appears to be a better alternative than prescribed burning Wyoming big sagebrush, largely because it leaves intact sagebrush, but comparisons between reference sites typically did not suggest habitat conditions were enhanced through mowing. Consequently, managers contemplating these 2 treatment techniques to enhance sage-grouse habitats should consider other treatment strategies including non-treatment.

When evaluating factors that may have influenced the probability of sage-grouse lek persistence in the Bighorn Basin we found support for the synergistic influence of multiple disturbance factors influencing sage-grouse lek persistence. We predicted that increasing roads, energy development, and wildfire will result in loss of more sage-grouse leks in the Bighorn Basin. The Bighorn Basin has lower developed reserves of oil and gas than many other regions of Wyoming; however, our study supports findings from studies in those areas that demonstrate energy development negatively affects lek persistence. We recommend that conservation efforts should focus on minimizing well development and implementing wildfire suppression tactics within 1.6-km of active sage-grouse leks.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

GENERAL INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) populations have experienced notable declines with the greatest decline occurring from the 1960s to the 1980s when populations decreased at an average yearly rate of 3.5% (Connelly et al. 2004). Populations currently occupy 56% of their historical distribution of potential habitat (Schroeder et al. 2004). These declines are primarily attributed to the loss, degradation, and fragmentation of sagebrush (*Artemisia* spp.) habitats (Braun 1998, Connelly et al. 2004). Recently, the U.S. Fish and Wildlife Service (2010) concluded that greater sage-grouse are warranted for protection under the Endangered Species Act of 1973, but because threats are moderate in magnitude and do not occur across their range at an equal intensity, the listing is precluded to other species under severe threat of extinction.

The declining status of sage-grouse may be due to a reduction in the quantity and quality of nesting and chick-rearing habitats, leading to low recruitment (Connelly and Braun 1997, Heath et al. 1997). The quality and quantity of sagebrush habitats have also declined over the last 50 years (Braun 1987, Connelly and Braun 1997). Disturbances such as livestock grazing (Patterson 1952, Beck and Mitchell 2000), prescribed burning (Nelle et al. 2000, Wambolt et al. 2001), wildfire (Connelly and Braun 1997, Connelly et al. 2000, Connelly et al. 2004), agricultural land use (Leonard et al. 2000, Knick et al. 2003, Smith et al. 2005), energy development (Lyon 2000, Aldridge and Boyce 2007, Walker et al. 2007, Harju et al. 2010), drought (Braun 1998), and herbicides (Connelly and Braun 1997) have been identified as primary contributors to the decrease of sagebrush communities and concomitant declines in sage-grouse populations.

Sage-grouse are associated closely with sagebrush habitats (Patterson 1952, Braun et al. 1977, Braun 1987). During winter months, November through April, sage-grouse diets consist almost entirely of sagebrush leaves (Patterson 1952, Remington and Braun 1985). Around May, grouse begin consuming forbs high in phosphorus, protein, and calcium (Barnett and Crawford 1994, Connelly et al. 2000). Structural features of perennial grass and sagebrush, such as cover and height, are used as protection from predators year-round, but are critical during the vulnerable nesting and early brood-rearing periods (Connelly et al. 2000, DeLong et al. 1995, Gregg et al. 1994). During nesting, mid-May to late June, females select sagebrush >30 cm in height and approximately 20% canopy cover (Connelly et al. 2000). Nesting female sage-grouse also often select perennial grass canopy cover >15% and >18 cm in height (Connelly et al. 2000).

During the first two weeks after hatching, chicks are dependent on insects, especially Coleoptera (beetles), Orthoptera (grasshoppers) and Hymenoptera (ants; Patterson 1952, Fischer et al. 1996). Studies have shown that insects make up about 60–75% of sage-grouse chick diets during this period (Patterson 1952, Peterson 1970, Johnson 1987). In a captive study, sage-grouse chicks did not survive if insects were absent from their diet within 4–10 days of hatching (Johnson and Boyce 1990). This same study suggested that insects contribute high levels of protein that aid in hatchling growth. Two weeks after hatching, chicks need a diet of forbs and insects that is high in species diversity for optimal growth (Patterson 1952). Vegetation recommendations for early brood-rearing include open stands of sagebrush with 10–25% canopy cover and about 15% canopy cover of grasses and forbs (Connelly et al. 2000). After about 3 months posthatch, juveniles focus on succulent forbs and incorporate sagebrush in their diets, which becomes their primary food during winter (Patterson 1952, Remington and Braun 1985, Drut et al. 1994).

Current management

Due to the degradation of sagebrush communities across the western United States, federal and state land management agencies have implemented numerous sagebrush management projects to promote land health (Hyder and Sneva 1956, Watts and Wambolt 1996, McDaniel et al. 2005), watershed improvement (Hibbert 1983, Dugas et al. 1998, Wilcox 2002), and wildlife habitat enhancement (Pyle and Crawford 1996, Wambolt et al. 2001, Crawford et al. 2004). The main vegetative objectives of treating sagebrush are to 1) reduce conifer encroachment (Holochek et al. 2004), 2) decrease mature stands of sagebrush (Perryman et al. 2002), 3) create a more diverse representation of seral stages across sagebrush landscapes (Davies et al. 2009), and 4) increase herbaceous cover by reducing competition between the herbaceous understory and sagebrush overstory (Dahlgren et al. 2006). Common treatment applications include 1) prescribed burning (Fischer et al. 1996, Wambolt et al. 2001), 2) mechanical removal (Connelly et al. 2000, Davies et al. 2009), and 3) chemical application (Johnson et al. 1996, Dahlgren et al. 2006). Prescribed burning and mechanical mowing treatments are two common techniques employed to enhance various aspects of sagebrush communities for nesting and early brood-rearing habitats for sage-grouse.

Prescribed burning has been used to improve biodiversity and forage quality for livestock as well as restore historical fire regimes (DiTomaso et al. 1999, Knick et al. 2003). Burning can lead to higher soil nutritional content, thus increasing plant production and understory biomass two years following fire (Rau et al. 2008). Prescribed fire can elicit positive short-term (≤ 10 years) response in the herbaceous understory in mountain big sagebrush (*A. tridentata vaseyana*) stands, but it does not elicit short-term positive herbaceous responses in Wyoming big sagebrush (*A. t. wyomingensis*) or long-term (> 10 years) positive herbaceous responses in Wyoming or mountain big sagebrush (Beck et al. *In Press*). The effects of fire on sagebrush communities are of particular importance as fire suppresses recovery of burned basin (*A. t. tridentata*), mountain, and Wyoming big sagebrush because these species do not resprout after fire (Pechanec et al. 1965, Tisdale and Hironaka 1981). Postburn recovery of Wyoming big sagebrush to preburn status is long (Wambolt et al. 2001); studies have shown recovery times lasting from 25 to over 100 years (Watts and Wambolt 1996, Wambolt 2001, Baker *In Press*, Beck et al. *In Press*). Wyoming big sagebrush is particularly vulnerable to fire because invasion of weedy exotics such as cheatgrass (*Bromus tectorum*) have led to increasing wildfire frequencies and subsequent loss and degradation of these important communities (Knick 1999, Baker *In Press*). Sagebrush communities are often left with a lack of litter and debris available for ground cover following prescribed burning, which lowers water infiltration especially during winter months (Shay et al. 2001). Litter-inhabiting insect species show high mortality rates when exposed to burning regimes (Panzer 2002). Ants have been shown to be more abundant in reference sites following prescribed burning (Fischer et al. 1996), while beetles have shown no difference between reference and treated sites (Pyle and Crawford 1996).

Mechanical treatments include aeration, anchor chaining, brush beating, harrowing, mowing, plowing, and rotocutting (Vallentine 1989). Mowing and other mechanical treatments are seen as alternatives to prescribed burning because they leave smaller live sagebrush plants after treatment (Davies et al. 2009), theoretically resulting in quicker recovery periods than those following burning. Our study focuses on the effects of mowing because treatment application is intended to thin sagebrush, not eliminate it, while also increasing the survival of young sagebrush and encouraging understory productivity (Davies et al. 2009). Mowing leaves residual debris used as cover by sagebrush-obligate wildlife (Dahlgren et al. 2006), reduces soil erosion (McKell 1989), and increases snow capture (Sturges 1989). Although mowing leaves residual sagebrush plants and woody debris, it reduces Wyoming big sagebrush cover and volume for about 20 years (Davies et al. 2009).

Bighorn Basin of Wyoming

Our study was conducted in the Bighorn Basin of north-central Wyoming (Fig. 1.1). This study area provided opportunities to investigate the influences of sagebrush treatments on sagebrush habitat quality and sage-grouse populations because: 1) there were abundant sage-grouse populations, which were monitored annually by the BLM and Wyoming Game and Fish Department (WGFD), providing a detailed data base to compare habitat conditions with populations; 2) treatment sites were typically readily accessible; 3) state and federal agencies were willing cooperators; and 4) there was a great need to conduct rigorous research in the Bighorn Basin to provide information to land management agencies and private entities managing nesting and early brood-rearing habitats for sage-grouse.

The Bighorn Basin is a plateau region and intermontane basin, approximately 160 km wide and 180 km long. The Basin has an average annual precipitation of 25.4 cm (National Climatic Data Center 2008). The Basin encompasses 32,000 km^2 in Bighorn, Hot Springs, Park, and Washakie Counties, Wyoming. Elevations range from 1220 to 1525 m; this lower elevation, relative to the rest of the state, results in the Bighorn Basin receiving an average of 90–120 frost-free days (Young et al. 1999); consequently, the Bighorn Basin is one of Wyoming's largest agricultural production areas, accounting for 27% of the value of crops produced in the state (National Agricultural Statistics Service 2009). Following the completion of the Buffalo Bill Dam and the introduction of irrigation in 1905, the Bighorn Basin developed into an agricultural area (Young et al. 1999). Major crops currently grown in the Bighorn Basin include spring wheat (*Triticum* spp), barley (*Hordeum vulgare*), oats (*Avena sativa* L.), dry beans (*Phaseolus* spp.), sugar beets (*Beta vulgaris* L.), alfalfa hay (*Medicago sativa*), and corn (*Zea mays*; Young et al. 1999).

The Cody and Worland BLM field offices manage >13,000 km² of public land and >17,000 km² of federal mineral estate (Bureau of Land Management 2008). About 70% of leks in the Bighorn Basin occur on Bureau of Land Management (BLM) land. About 25% of the Bighorn Basin is privately owned. By comparison, the proportion of public land in the Bighorn Basin is very similar to the amount of public land (~70%) providing the remaining habitat to sage-grouse across their range (Knick et al. 2003).

Sage-Grouse in the Bighorn Basin of Wyoming

Currently there are 256 known sage-grouse leks in the Bighorn Basin (Wyoming Game and Fish Department, unpublished data, 2009). Lek survey data, used to determine if leks are active during the breeding season, have been collected since 1958 (Wyoming Game and Fish Department, unpublished data, 2009). Current standardized monitoring, lek counts, have been implemented since 1998. These counts are used to record the maximum number of males attending active leks where counts consist of at least 3 visits to each lek during the breeding season and conducted at least 7 days apart (Wyoming Game and Fish Department, unpublished data, 2009). Recent work in the Bighorn Basin reports peak female attendance around 9 April each year and male peak attendance around 13 April each year (Harrell 2008), which is relatively a week earlier than other portions of Wyoming at higher elevations (Patterson 1952). Brood counts have been conducted since 2000 where Wyoming Game and Fish Department personnel surveyed areas thought to be occupied by brood-rearing grouse and where they have recorded numbers of chicks, female, and male sage-grouse. There were on average 3.5 chicks per hen and 4.3 chicks per brood during July and August from 1962–2006, however sample sizes were small (<25 groups) and averaged across the Basin (Big Horn Basin Working Group 2007). However, research focusing on behavior, habitat selection, or demographic parameters of sage-grouse in the Basin is lacking.

Between 1948 and 2007, harvest of sage-grouse has ranged from a low of 365 in 2003 to a high of 8,535 in 1977 (Big Horn Basin Working Group 2007). Traditionally, hunting seasons for sage-grouse opened in late August or early September. In 1995, the Wyoming Game and Fish Commission instituted smaller bag limits and shorter seasons (3 birds/day and 6 birds in possession) that resulted in lower harvest due to seasonal changes (Heath et al. 1997). Currently hunting seasons start later in September (third or fourth Saturday) and close in late September or early October, with 2 birds per day and 4 birds in possession (Wyoming Game and Fish, unpublished data, 2009). The Wyoming Game and Fish Commission (2002, unpublished data) suggested hunting seasons be closed if the population of grouse is less than 300 birds. The lack of data and field studies in the Bighorn Basin makes estimating sage-grouse population size difficult. Managers will not suspend hunting until continuous surveys on accessible leks indicate that combined male and female counts are less than 300 adult sage-grouse. Hunting is not seen as the primary cause of rangewide sage-grouse declines; rather, invasive species, infrastructure (i.e. roads, powerlines and pipelines), oil and gas development, and wildfire are some of the top threats to sage-grouse (USFWS 2010).

PURPOSE

The purpose of our research was twofold. First, we evaluated differences in response variables that are known to be important to sage-grouse reproduction and survival as influenced by prescribed burning and mowing in Wyoming big sagebrush communities in the Bighorn Basin of Wyoming. We focused this portion of our research on nesting and brood-rearing habitats because the quality of these areas may be driving sage-grouse population declines through negatively affecting nest success and juvenile survival (Beck et al. 2003, Crawford et al. 2004, Beck et al. 2006). Our research findings provide insights on how sage-grouse nesting and early brood-rearing habitats in Wyoming big sagebrush were affected following prescribed burning and mowing (Chapter 2). Secondly, in an effort to examine sage-grouse populations in the Bighorn Basin, we identified disturbances contributing to the decline in lek persistence in the Basin (Chapter 3).

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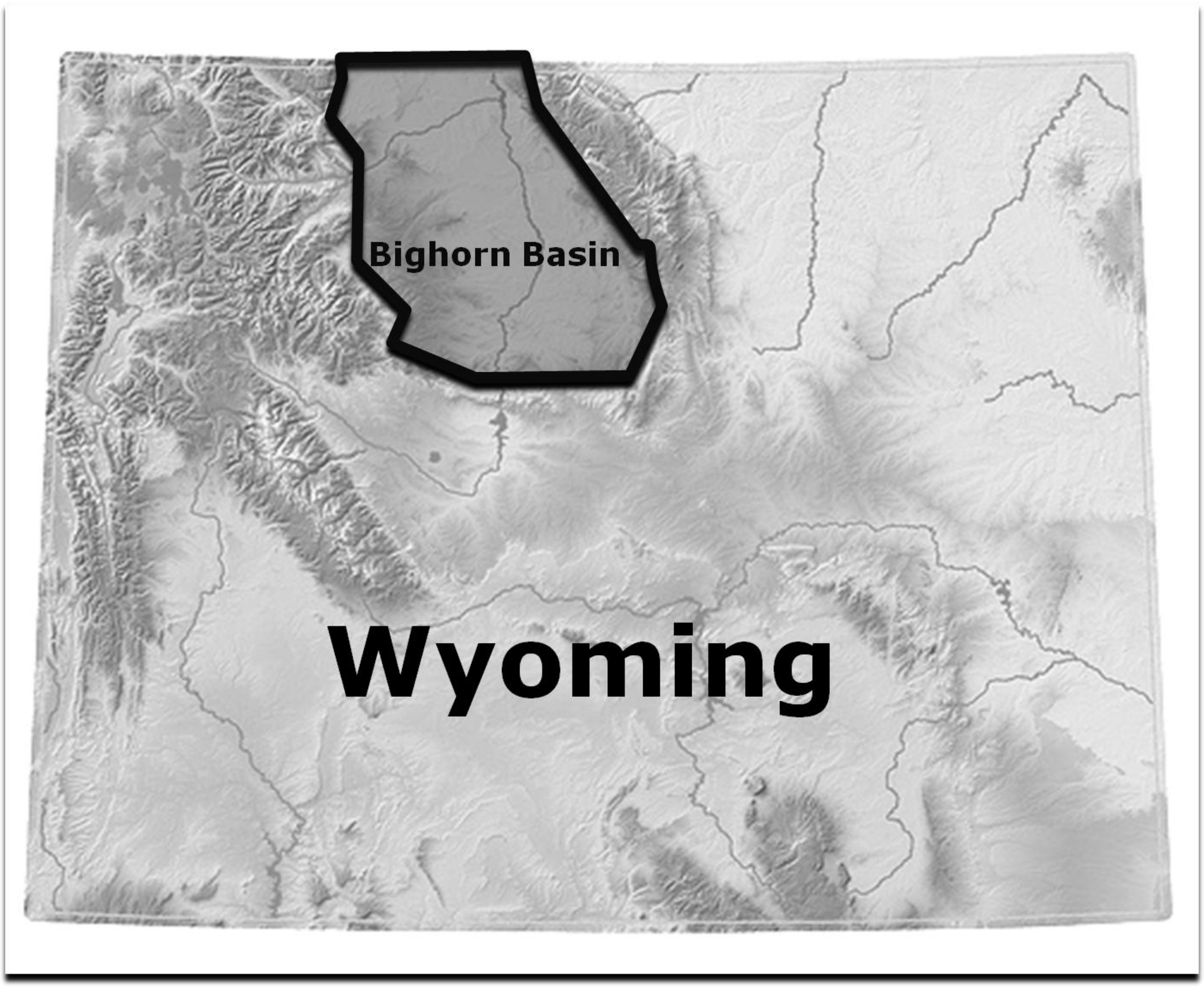

Figure 1.1. Map of Wyoming with outline of the Bighorn Basin in north-central Wyoming, USA. Geographic data provided by the Wyoming Geographic Information Science Center.

CHAPTER 2

COMPARISON OF PRESCRIBED BURNING AND MOWING TO ENHANCE GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) NESTING AND EARLY BROOD-REARING HABITAT IN THE BIGHORN BASIN, WYOMING

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ABSTRACT

Bureau of Land Management field offices have implemented over 190 km² of prescribed burns since 1980 and over 90 km² of mowing treatments since 2000 in an effort to enhance Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) habitats in the Bighorn Basin of north-central, Wyoming. Objectives of these treatments have focused on land health, watershed improvement, and to enhance habitat conditions for livestock, greater sage-grouse (*Centrocercus urophasianus*), and other wildlife. Although fire may stimulate short-term herbaceous response, it is recognized as a key factor contributing to the decline of sage-grouse populations and can suppress recovery of Wyoming big sagebrush. Mowing has been suggested as an alternative to prescribed burning because mowing leaves young sagebrush plants and residual debris that can reduce soil erosion, increase snow capture, and be used as cover by wildlife from predatory species. We initiated our study in spring 2008 to compare prescribed burning and mowing to enhance sage-grouse nesting and brood-rearing habitats within Wyoming big sagebrush communities in the Basin. We evaluated habitat quality through insect, soil, and vegetation parameters at 30 treated sites compared to 30 nearby, untreated reference sites. Our sites were classified by treatment type, soil type, season, and decade of treatment (sites burned in the 1990s and sites burned or mowed during 2000–2006). Our objectives were to evaluate differences in

structural and functional parameters known to influence ecological function and sage-grouse population parameters. Prescribed burning greatly (–85.1 to –100%) reduced levels of sagebrush canopy cover at least 19 years postburn, while mowing maintained minimum levels of sagebrush canopy cover recommended for sage-grouse nesting and early brood-rearing habitats. In some cases, prescribed burning showed positive results for sage-grouse nesting and early brood-rearing habitats compared to mowing such as 6.3- to 16.9-times greater ant weights (mg/trap; on burned sites on aridic soils during the 1990s and burned sites on ustic soils during 2000–2006 respectively), 2.3- to 85.1-times greater beetle weights (mg/trap) on ustic soils, 3.6- to 4.3-times higher perennial grass canopy cover on aridic soils, 2.6-times higher plant species richness on aridic soils during 2000–2006 burns, and 2.0- to 5.0-times higher soil nitrogen on burns during 2000–2006, but all of these characteristics were not found to be enhanced compared to reference sites. Mowing provided 3.6- to 13.2-times higher sagebrush canopy cover on ustic soils, 2.2- to 3.0-times higher sagebrush heights on aridic and ustic soils, and 1.2- to 1.5-times higher insect diversity on ustic and aridic soils than prescribed burning. When comparing mowed sites to reference sites, mowed sites had 2- to 2.5-times higher litter on aridic soils and 3.5- to 9.1-times higher ant weights (mg/trap) on ustic soils. However, mowing did not promote an increase in other sage-grouse early brood-rearing needs such as the abundance of food forbs, abundance or weights of beetles and grasshoppers, or perennial grass canopy cover or height. Forb nutritional content and production at treatment sites were similar to reference sites. We found higher bare ground at mowed sites compared to burned sites (1.1- to 30.8-times higher than prescribed burned sites on aridic soils). Perennial grass height and canopy cover (5 of 6 cases; Appendix 2.C) were not enhanced through burning or mowing. The main benefit from prescribed burning was an increase in grasshopper abundance (no./trap) compared to reference sites (grasshopper abundance was 2.4- to 3.4-times greater at prescribed burned sites than reference sites). Grasshopper abundance at mowed sites was not different than at reference sites. Contrary to desired outcomes following treatment, the reduction of Wyoming big sagebrush canopy cover through prescribed burning or mowing may not stimulate growth of herbaceous understory. Our findings are supported by other studies showing minimal or no improvement of structural features, herbaceous responses, and insect abundance and diversity following treatment in Wyoming big sagebrush communities. In the Bighorn Basin, prescribed burning and mowing Wyoming big sagebrush have resulted in few positive aspects for enhancing habitat conditions for sage-grouse nesting and early brood-rearing 19 and 9 years post-treatment, respectively. Consequently, managers contemplating applications of these 2 treatment techniques to enhance sage-grouse habitats should consider other treatment strategies including non-treatment.

INTRODUCTION

Big sagebrush (*Artemisia tridentata*) communities provide habitat for 93 bird, 92 mammal, and 58 reptile and amphibian species (Welch 2005). The loss of large expanses of sagebrush have led to declines in >350 sagebrush associated plants and animals (Rowland and Wisdom 2005) including greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse; Braun 1998, Knick et al. 2003, Connelly et al. 2004), which have lost 50–60% of their historical habitat (Schroeder et al. 2004). State and federal agencies have implemented sagebrush enhancement techniques in efforts to improve remaining stands of sagebrush for land health (Hyder and Sneva 1956, Watts and Wambolt 1996, McDaniel et al. 2005), watershed improvement (Hibbert 1983, Dugas et al. 1998, Wilcox 2002), increasing forage for livestock (Vale 1974, Beck and Mitchell 2000), and wildlife habitat enhancement (Pyle and Crawford 1996, Wambolt et al. 2001, Crawford et al. 2004). Vegetation goals for treating sagebrush include, but are not limited to 1) reducing conifer encroachment (Holechek et al. 2004), 2) decreasing mature stands of sagebrush (Perryman et al. 2002), 3) creating a more diverse representation of seral stages across sagebrush landscapes (Davies et al. 2009), and 4) increasing herbaceous cover by reducing competition between the herbaceous understory and sagebrush overstory (Dahlgren et al. 2006).

Burning programs have been conducted by land management agencies to enhance habitat conditions for sage-grouse (Fischer et al. 1996, Wambolt et al. 2001), yet fire has been identified as one of the primary factors leading to range-wide declines in greater sage-grouse populations (Connelly and Braun 1997). Annual grasses, particularly cheatgrass (*Bromus tectorum*), often invade or expand in xeric sagebrush landscapes following fire, where the fine fuels they accumulate increase fire frequencies (West 2000, Baker *In Press*). Soil nitrogen can be increased following prescribed burning and influence the regrowth of native plants, encourage invasion of invasive species, and influence overall site recovery (Rau et al. 2007). Fire may increase short–term (≤ 10 years) perennial grass and forb production in mountain big sagebrush (*A. t. vaseyana*; Beck et al. *In Press*), but fire suppresses recovery of burned basin (*A. t. tridentata*), mountain, and Wyoming big sagebrush (*A. t. wyomingensis*) because these species do not resprout after fire (Pechanec et al. 1965, Tisdale and Hironaka 1981). Wyoming big sagebrush is particularly vulnerable to fire because invasion of weedy invasives such as cheatgrass have led to increasing wildfire frequencies and subsequent loss and degradation of these important communities (Baker *In Press*). The effects of prescribed burning are better understood than those induced through mowing, with positive (Wambolt and Payne 1986, Perryman et al. 2002), neutral (Peek et al. 1979, Wambolt and Payne 1986, Fischer et al. 1996, Wambolt 2001, Perryman et al. 2002, Wrobleski and Kauffman 2003), and negative (Peek et al.

1979, Wambolt and Payne 1986, Fischer et al. 1996, Wambolt 2001, Wrobleski and Kauffman 2003) effects to nesting and early brood-rearing habitat in burned Wyoming big sagebrush.

Sagebrush is essential to maintaining native plants and limiting invasion of invasive plants in sagebrush communities (Prevéy et al. 2010, Reisner 2010). This suggests that treatments should be limited to those that do not eliminate or greatly reduce sagebrush. Mowing and other mechanical treatments are seen as alternatives to prescribed burning because they leave smaller live sagebrush plants after treatment (Davies et al. 2009), and recovery following burning in mountain big sagebrush may take 25–100 years and recovery of Wyoming big sagebrush following burning is often much slower and can be highly variable (Baker *In Press*). Fire rotations in Wyoming big sagebrush range in frequency from 200 to 350 years and are dependent on climate, topography, plant composition, and ecological site characteristics (Baker *In Press*).

Mowing leaves residual debris used as cover by sagebrush-obligate wildlife (Dahlgren et al. 2006), reduces soil erosion (McKell 1989), and increases snow capture (Sturges 1977). Although mowing leaves residual sagebrush plants and woody debris, it reduces Wyoming big sagebrush cover and volume for about 20 years (Davies et al. 2009). Comparing response variables collected at mowed and prescribed burned sites provides a way to better understand which sagebrush-reduction treatment may be most suitable to enhance particular aspects of sage-grouse habitats.

Within Bureau of Land Management lands in the Bighorn Basin, there has been an active burning program since 1980 to enhance diversity and production of herbaceous vegetation, while also promoting land health and watershed improvement (Jack Mononi, Cody BLM and Tim Stephens, BLM Worland Field Office, personal communication, 2009). Mowing programs have been conducted since 2000 in an effort to enhance age class diversity and stimulate regeneration of Wyoming big sagebrush. Wildfires have also affected large areas of sagebrush steppe particularly in the southeastern portion of the Bighorn Basin. From 1980 to 2009, the USDI-Bureau of Land Management conducted 156 prescribed burns (100 km^2 burned) and 55 mowing treatments (36 km^2 mowed) in big sagebrush communities to reach vegetation management objectives, including enhancing habitat conditions for sage-grouse. By comparison, 91 wildfires have burned 520 km^2 of sagebrush since 1980. The numerous wildfires, prescribed burns, and mowing treatments that have occurred within the Bighorn Basin since 1980 (Fig. 2.1) provide opportunities for replicated field studies or field experiments, which provide larger inferential space and stronger conclusions than other quasi-experimental designs such as case studies or natural experiments that are limited to unreplicated disturbance events (Garton et al. 2005).

Our objectives were to evaluate differences between 1) structural response variables and 2) variables that reflect functional ecological processes that influence sage-grouse reproduction and survival within mowed and prescribed burned Wyoming big sagebrush communities in the Bighorn Basin, Wyoming. Structural response variables included herbaceous nesting cover and shrub-structural features. Functional process variables included grouse forage availability and quality (i.e., forbs and insects) and ecological function (i.e. bare ground and soil quality) of sagebrush communities. Our fundamental research questions were: 1) Do mowed and prescribed burned Wyoming big sagebrush communities provide lower levels of structural ecological parameters known to be important to sage-grouse survival and reproduction than their paired, untreated reference sites? 2) Do mowed Wyoming big sagebrush communities provide higher levels of structural ecological parameters known to be important to sage-grouse reproduction and survival than sagebrush communities that were prescribed burned? 3) Do response variables reflecting ecological function occur at higher levels in mowed than in Wyoming big sagebrush that has been prescribed burned?

STUDY AREA

The Bighorn Basin includes Big Horn, Hot Springs, Park, and Washakie Counties and encompasses 32,002 km^2 of north-central Wyoming. The Bighorn Basin is bordered by the Absoraka Mountains to the west, Beartooth and Pryor Mountains to the north, Bighorn Mountains to the east, and Bridger and Owl Creek Mountains to the south. The average valley elevation is 1,524 m (1,116 m minimum) and is composed of badland topography and intermittent buttes. The Bighorn Basin is semi-arid with average annual precipitation ranging from 12.7–38.1 cm with most precipitation occurring in April and May as rain. Dominant land uses in the sagebrush areas between agricultural lands and forest lands in the Bighorn Basin include livestock grazing; limited bentonite mining, with most current extraction occurring in lower elevation saltbush (*Atriplex* spp.) desert; and oil and gas extraction.

The native flora of the Bighorn Basin includes perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*), Indian rice grass (*Achnatherum hymenoides*), needle and thread (*Hesperostipa comata*), and western wheatgrass (*Pascopyrum smithii*); shrubs such as Wyoming (*Artemisia tridentata* ssp.*wyomingensis*) and mountain big sagebrush (*A. t*. ssp. *vaseyana*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.), and spineless horsebrush (*Tetradymia canescens*); and forbs/subshrubs including buckwheat (*Eriogonum* spp.), desert parsley (*Lomatium* spp.), milkvetch (*Astragalus* spp.), globemallow (*Sphaeralcea* spp.), prairie sagewort (*A. frigida*), pussytoes (*Antennaria* spp.), sego lily (*Calochortus nuttallii*), and Western yarrow

(*Achillea millefolium*). Invasive species in the Basin include cheatgrass (*Bromus tectorum*), Japanese brome (*B. japonicus*), Canada thistle (*Cirsum arvense*), hoary cress (*Cardaria draba*), and toadflax (*Linaria* spp.).

METHODS

The observational units (study sites) in our study were 3, 100-m x 1-m transects placed within treated sites defined by combinations of soil group, age since treatment by decade (1990–1999 and 2000–2006), and treatment type. We refer to these combinations as chronosequences, which are hypothetical portrayals of soil change as a function of time (Fanning and Fanning 1989). General soil groupings that comprise the soils in the Bighorn Basin are aridic, fine textured; aridic, coarse textured/skeletal; udic, cryic; and ustic, frigid (Fig. 2.2). We based these groupings on soil temperature, moisture, and texture, which largely influence establishment and development of sagebrush communities in the Bighorn Basin (Young et al. 1999; Larry C. Munn, University of Wyoming, personal communication, 2007).

We removed from consideration, treatment combinations 1) that had fewer than 3 treated polygons, 2) that were conducted from 2007–2008 because we did not want to bias results by examining short-term responses commonly found 2 years post-burn (McGee 1982, Hobbs and Spowart 1984), 3) that occurred on aridic, coarse textured/skeletal soils because these soils often supported alkaline-adapted communities, which were not typically used by sage-grouse, and 4) that occured on udic, cryic soils because these soils typically supported forested habitats. In addition, the distribution of sage-grouse leks throughout the Bighorn Basin indicated habitats overlying aridic, coarse textured/skeletal and udic, cryic soils were not selected by grouse during the breeding season (Fig. 2.2). Consequently, much of the nesting and early brood-rearing activity of sage-grouse in the Bighorn Basin was centered on areas overlying aridic, fine textured and ustic, frigid soils (Fig. 2.2), which we retained for consideration.

We randomly selected 3 treated polygons from each treatment combination for field sampling in spring 2008. To provide comparative sites, we selected 1 untreated reference site near each randomly-selected treated polygon. The mean distance from treatment sites to paired reference sites was 408 m (range: 146–1,475 m). Research in Wyoming has shown the majority (64%) of sage-grouse nesting may occur within 5.0-km of leks in contiguous habitats (Holloran and Anderson 2005). To ensure sampling sites were accessible habitats for sage-grouse, the average distance from treated and reference sites to nearest known sage-grouse leks was 4.5 km (range: 0.2–11.8 km). To avoid extraneous effects, we did not consider untreated sites that were noticeably degraded, damaged, or destroyed. Although untreated sites that are not degraded, damaged, or destroyed will undoubtedly exhibit effects of past land management practices (e.g., livestock and wildlife herbivory), we assumed they represented the potential of the surrounding landscape to provide vegetation structure and ecological function as would be expected given common grazing disturbance mechanisms that affect much of the Bighorn Basin. During the 2008 field season, we sampled 30 treated sites (3 replicate treated sites × 10 treatment combinations) and 30 nearby untreated, reference sites (one reference site for each selected treatment combination site) for a total of 60 sites.

Considerations in Selecting Sampling Sites

Many factors likely influence recovery of treated sites including conditions under which treatments were conducted, and history since treatment including herbivory since treatment. These are difficult issues to address because they may potentially influence the development of sagebrush communities following treatment. Through conversations with Bureau of Land Management biologists (J. Mononi, D. Saville, T.Stephens and C. Whalley, Bureau of Land Management, personal communication, 2008), we learned that some information may be available to better understand post-treatment livestock grazing management. However, numerous changes in management limited this information. We concluded, after thorough investigation, that categorizing sagebrush treatments in relation to grazing management was not possible; therefore, we did not include grazing as a treatment factor. However, improved livestock grazing management practices have been implemented in the Bighorn Basin in the last two decades, leading to improved rangeland conditions—these changes have likely elicited a positive vegetative response to treated and untreated Wyoming big sagebrush communities (J.Mononi, BLM Cody Field Office, personal communication 2010). Findings from our study thus likely reflect vegetation responses associated with improved grazing practices; however, they should not affect comparisons between mowing and prescribed burning or between treatment and reference sites. We did assess whether grazing had occurred at each site prior to sampling, but found minimal to no evidence that it had occurred. This is important to note because some cattle grazing had occurred in 2008 at 4 of our sites prior to field sampling (J. Mononi, BLM Cody Field Office, personal communication 2010).

Prior to selecting sampling units and initiating field work, we gathered information from Bureau of Land Management records to populate treatment records with auxiliary information to better inform our selection of sampling sites. Many treatments (38 treatments out of 269) were not considered as potential observational units because burns were not intended to kill sagebrush or were located in areas that were not potential sage-grouse nesting or early brood-rearing habitat (i.e., areas surrounded by conifers, high elevations, or areas dominated by greasewood). In addition, some of these burns were designed to accomplish objectives that were not specific to enhancing sage-grouse habitat, for example juniper [*Juniperus* spp.] encroachment and aspen [*Populus tremuloides*] habitat improvement. Reviewing existing records assisted in determining the set of treatments that formed the list of observational units from which random selection for each treatment combination was possible.

Because burning and mowing has occurred irregularly across the Bighorn Basin (Fig. 2.1), our sampling locations needed to reflect a spatially balanced (i.e., geographically distributed) selection of sampling sites. To ensure a spatially balanced sample, we used Program S-Draw (Western Ecosystems Technology, Incorporated, Cheyenne, Wyoming 82001 USA) to select sampling sites using the UTM coordinates of each treatment location in a generalized random tessellation stratified sample (Fig. 2.1).

Field Sampling

In spring 2008, we established 3, 100-m x 1-m transects in 30 treated and 30 untreated sites to facilitate field sampling. We placed 3, parallel 100-m surveyors' tapes extending N-S and spaced 50-m apart starting at a randomly determined point in each treatment site, no closer than 50 m from the nearest untreated edge to avoid edge effects (Fig. 2.3). The 3, 100-m surveyors' tapes formed the basis for sampling insect, soil, and vegetation parameters. At sites where sagebrush had been mowed in strips, we placed 1, 100-m surveyors' tape in 3 mowed strips at an average spacing of 55 m (range: 32–93 m). Ideally we would have maintained 50-m spacing between strips, however due to the irregular pattern of mowing, 3 sites were spaced 32–35 m apart. We placed identical transects at random locations for all treatments within untreated reference polygons (mean distance 624-m [range 146–1,475 m]). We selected reference sites by using a random numbers table to obtain a random distance and direction from each treated site in which to establish each reference site.

Insect Sampling

We collected arthropods (insects and spiders) at the same time as vegetation sampling at each treatment and reference location in 2008 and 2009 to evaluate insect abundance and diversity among habitat treatments during the early brood-rearing period (Connelly et al. 2003). We collected ground-dwelling arthropods with pitfall traps (Ausden and Drake 2006) and grass and forb-dwelling arthropods with a 0.4-m diameter sweep net (Fischer et al. 1996).

We placed 10 pitfall traps filled with 95% propylene glycol (SIERRA® antifreeze, Peak™ Performance Products, Old World Industries, 4065 Commercial Avenue, Northbrook, IL 60062 USA) and 5% water flush with the ground and 2 m to the west of each transect at 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 m marks along each of the 3, 100-m transects (Fig. 2.3). Propylene glycol-based antifreeze is advantageous over ethylene glycol-based antifreeze because it is less toxic to children, pets, and wildlife. We left covers off pitfall traps from the morning to the evening of the next day, to capture arthropods during 2 diurnal periods (Fischer et al. 1996).

We used sweep nets to collect arthropods between 2 and 5 m west of, and parallel to, each transect mark where pitfall traps were placed. Each sweep net sample consisted of 100 sweeps through grass and forb canopy or the tops of shrubs parallel to each transect, between pitfall traps (10 m spacing; Fig. 2.3). To facilitate sorting in the lab, we placed sweep net samples directly into labeled plastic bags and stored them on ice until frozen. Our sampling procedures thus provided 30 samples of arthropod fauna from the ground and herbaceous or shrub layers from both collection techniques at treatment and reference sites.

We preserved arthropod samples in plastic vials filled with 70% ethanol prior to laboratory analyses (Fischer et al. 1996). In the laboratory, insects (Class Insecta) were separated from shrub detritus, vegetation, and other arthropods. Insects from each 10-m sample were sorted to Order, using a dichotomous key, and then weighed and counted. Separating insects important to sage-grouse (Hymenoptera [ants], Coleoptera [beetles], and Orthoptera [grasshoppers]) allowed us to estimate composition and biomass for each treatment site. After counting and weighing insect collections, we computed Shannon's diversity index and Pielou's evenness index to assess insect diversity and evenness among treatment and reference sites (Krebs 1999).

Soil Quality (Total, Organic, and Inorganic Carbon and Nitrogen) Sampling

We collected soil samples from mid-June to early July 2009, 1-m from tapes at 20, 40, 60, 80, and 100 m marks along each of the 3, 100-m transects established at each treatment and reference site, yielding 15 soil subsamples per site (Fig. 2.3). We collected soil samples from a depth of 10 cm using a marked hand trowel. We then prepared a composite bulk sample from the soil subsampled at each site by placing the 15 soil subsamples in a bucket, thoroughly mixing, and then bagging 1 quart of soil for laboratory analyses. We placed all composite samples in labeled plastic bags, air dried them, and stored them at the University of Wyoming Research Extension Center in Powell, Wyoming until returning from the field. Once soil samples were brought back to the lab, we ground them with mortar and pestle, sieved them through a 2 mm sieve, and ground them once again. Samples were separated into 3 separate plastic bags for (1) total carbon and nitrogen, (2) inorganic carbon and, (3) nitrate and ammonia analyses.

We extracted soil inorganic nitrogen with a 0.5 M KCl solution, with the extracts analyzed on a Traacs auto-analyzer to determine the fraction of $NO3^{-}$ and $NH4^{+}$ (Robertson et al. 1999). We determined total carbon and nitrogen content of finely ground subsamples using an Elementar automated combustion analyzer (Nelson and Sommers 2001). We quantified soil inorganic carbon using the modified pressure calcimeter method (Sherrod et al. 2002). We calculated soil organic carbon as the difference between total carbon and inorganic carbon (Nelson and Sommers 2001).

Vegetation Sampling

We collected vegetation data from late May to early July in 2008 and 2009. In both years, we initiated data collection at lower elevations and then moved to higher elevation sites to follow the nesting and early brood-rearing altitudinal pattern of adult hens with their broods. Along the middle tape, we measured height (cm) of grasses (droop height) and shrubs (tallest leader), total gap (i.e., percentage of surveyors' tape without vegetated canopy cover), and composition of shrub species composing the treatment location (Fig. 2.3). We measured shrub elliptical area (E; cm) by using the equation provided by Wambolt et al. (1994), to compute shrub elliptical area as $E = \pi \times (MJ \times 0.5) \times (MN \times 0.5)$. The major axis (MJ) was found by measuring the horizontal distance across only living plant material of the shrub and the minor axis (MN) was measured as the maximum width of living shrub material perpendicular to the horizontal axis. We calculated shrub canopy cover by using the MJ and MN axes to find the area of an ellipse to compute shrub crown (cm^2) areas. Then, we took the total number of shrubs per belt transect and multiplied that number by the average crown area of shrubs measured. We calculated the % canopy cover by the total cover of shrubs divided by the belt area (belt = 1 m x 100 m = 100 m^2 = 1,000,000 cm^2)

and multiplied by 100 (total cover of shrubs/1,000,000 $cm^2 \times 100$) to yield percent canopy cover. At each 5-m mark along each middle 100–m tape, we positioned a 20 × 50 cm quadrat to ocularly estimate cover of bare ground, biological soil crust, forbs, grasses, litter, and rock according to 7 cover classes : **1**= 0–1% **2** = 1–5%; **3** = 5–25%; **4** = 25–50%; **5** = 50–75%; **6** = 75–95%; **7** = > 95% (Daubenmire 1959).

We tabulated cover of perennial forbs that are important for food or habitat for insects eaten by sage-grouse (Table 2.2). Our list of perennial food forbs was developed after visiting field sites and consulting relevant sources (Patterson 1952, United States Forest Service, 2002, Wyoming Game and Fish Department, 2002, Beck et al. 2009).

To assess forage quality during early brood-rearing (late May to mid-June) we positioned a 20 × 50 cm quadrat to the west of each 10, 20, 30, 40, 50, 60, 70, 80, 90, and 100 m mark from the starting point along the east and west surveyors' tape in spring 2008. We positioned a 20 × 50 cm quadrat to the west of each 5, 15, 25, 35, 45, 55, 65, 75, 85, and 95-m mark of the surveyor's tape in spring 2009 to avoid clipping the same location clipped in 2008 (Fig. 2.3). In each of the 20 quadrats we clipped and weighed all perennial food forbs to ground level, initially air dried them, then oven dried them for 48 hours at 60° C and then ground these samples to 1 mm size for standing crop (kg/ha), gross energy (kcal/kg DM), crude protein (%), phosphorous (%), and calcium (%) analyses (Barnett and Crawford 1994). Each year we combined ground samples across each transect to provide 2 composited food forb samples for each treated and reference site. Samples were apportioned into 3 envelopes (1 sample was retained, and 2 samples were sent to separate laboratories for analyses). Samples weighing 2 g were submitted to the Wildlife Habitat and Nutrition Lab at Washington State University, Pullman, Washington, 99163 USA (contact: Dr. Bruce Davitt) for crude protein and gross energy analyses. Calcium and phosphorus were analyzed by dry ashing (Galvak et al. 2005) at the University of Wyoming Soil Testing Laboratory, Laramie, Wyoming, 82071, USA. Nutritional values from these composited forage samples reflected nutrient levels in food forbs found at each site.

Experimental Design and Data Analyses

We collected data at 5 burned sites in mountain big sagebrush communities and removed them from our analysis to focus on Wyoming big sagebrush communities. After conducting two-sample *t*-tests ($P < 0.05$; PROC TTEST, SAS Institute 2003) for each response variable, we found no difference between fall and spring burned treatment combinations, which permitted us to combine these combinations for prescribed burned treatments. Therefore, we grouped prescribed burned sites by soil type and decade of use and mowed sites by soil type. These considerations allowed us to retain 6 treatment combinations across years: 1) sites that were mowed on aridic soils ($n = 3$), 2) sites that were mowed on ustic soils ($n = 3$), 3) sites that were prescribed burned during the 1990s on aridic soils ($n = 6$), 4) sites that were prescribed burned during the 1990s on ustic soils ($n = 6$), 5) sites that were prescribed burned during 2000–2006 on aridic soils ($n = 3$), and 6) sites that were prescribed burned during 2000–2006 on ustic soils ($n = 4$).

We analyzed results from our 6 treatment combinations as a two-factor ANOVA set in a completely randomized design. By including a site term in the analysis, our working linear statistical model was: $Y_{ijk} = \mu + Trt_i + S_k + \varepsilon_{ijk}$, where Trt_i = the i^{th} treatment type, S_k= the k^{th} site and ε_{ijk} = experimental errors. For the treatment factor, we tested the null hypothesis that, for any given response variable, treatment means were the same versus the alternate that at least 2 treatment means were different (Oehlert 2000). If the null hypothesis was rejected (P <0.05), we further investigated the influence of treatment type, decade of treatment, and soil grouping using linear contrasts. We made the following nonorthogonal comparisons: 1) mowed and prescribed burned sites compared to reference sites, 2) prescribed burned sites during the 1990s compared to sites that were prescribed burned during 2000–2006, 3) mowed sites compared to sites that were prescribed burned in the 1990s, 4) mowed sites compared to sites that were prescribed burned during 2000–2006 , 5) mowed sites compared to sites that were prescribed burned on aridic soils, and 6) mowed sites compared to sites that were prescribed burned on ustic soils. We adjusted *P*–values (<0.05 to <0.008) with the standard Bonferroni correction to protect the experiment wise error rate (Keppel 1991). For the site factor, we tested the null hypothesis that the treated sites were the same as their corresponding reference sites versus the alternate that at least two differed.

An important component of our study was to develop a catalog of effect sizes to be used in future manipulative experiments. We identified 33 response variables representing various aspects of greater sage-grouse habitat quality including ecological status, grouse forage, soil quality, and vegetation structure (Table 2.1). We computed effect sizes to compare prescribed burned sites to mowed sites and prescribed burned and mowed sites to their respective reference sites. Our effect sizes were computed as: 1) means across burned sites during 2000–2006 (X) – means of mowed sites (Y): 2) means across burned sites during the 1990s (X) – means of paired reference sites (Y): 3) means across burned sites during 2000–2006 (X) – means of paired reference sites (Y): and 4) means across mowed sites during 2000–2006 (X) – means of paired reference sites (Y). We computed the standard errors (SE) for effect sizes:

$SE[X-Y] = \sqrt{var[X-Y]} = \sqrt{SE^2{}_x + SE^2{}_y}$. Using the SEs for each effect, we computed 95% confidence intervals for effect sizes for each habitat feature. Confidence intervals that included zeros indicated effect sizes that were not statistically significant. Negative effect sizes indicated the response in habitat features was lower at burned sites than mowed sites or lower at treated sites than reference sites. Positive effect sizes indicated response in habitat features at burned sites was higher than at mowed sites or higher at treated sites compared to reference sites. Effect sizes of 0.0 indicated equal responses in sage-grouse habitat features across comparisons. We performed statistical analyses with statistical analysis software (SAS; SAS Institute 2003) with statistical significance set at $\alpha = 0.05$. We only report effect sizes with mean and SE when specific treatment combinations were significant across more than 1 treatment combination (refer to Appendices 2.A and 2.B for these results).

We used principal components analysis (PCA) on the habitat variable correlation matrix to reduce the dimensionality and identify meaningful underlying variables in our set of habitat response variables using statistical software (SAS; SAS Institute 2003). We selected the first 3 principal components (PC) to interpret our data matrix because they provided a balance between interpretability of results and the amount of variability explained (Johnson 1998). We plotted PC scores on PC axes according to years to assess which treatments had noticeably different responses in insect, soil, and vegetation characteristics. Because we sampled soil characteristics in 2009, we used the same carbon and nitrogen estimates in PCA analyses for both years.

RESULTS

We collected field data at 30 treated and 30 reference sites across summers 2008 and 2009 to provide data from 120 sites. In total, we sorted, counted, and weighed 7,040 insect samples; analyzed 112 food forb samples for crude protein, net energy, calcium and phosphorus; and analyzed 60 soil samples for total carbon, nitrogen, organic carbon, inorganic carbon, nitrate, and ammonium. These totals include data collected at 5 mountain big sagebrush sites; however, data at the mountain big sagebrush sites are not reported. We rejected the null hypothesis for 17 of the 30 two-factor ANOVAs we considered and further investigated the influence of treatment type, decade of treatment, and soil grouping using linear contrasts for these models. Below we report major findings from both years for effect sizes and linear contrasts, however, we encourage readers to consult Appendix 2.A (mean and SE for all response variables and treatment combinations) to evaluate the magnitude of differences among response variables at treated and reference sites; Appendix 2.B (significant effect sizes in prescribed burning compared to mowing) and Appendix 2.C (significant effect sizes in prescribed burning and mowing compared to reference sites) for effect size results; and Appendix 2.D for significant linear contrast results.

Effect Sizes

There were no significant effect sizes (95% confidence intervals overlapped 0.0) between treatment and paired reference sites for annual brome canopy cover, annual forb canopy cover, ant weights, beetle counts, beetle weights, food forb canopy cover, food forb species richness, Shannon’s diversity index for foliage-dwelling insects based on weights, nonfood forb canopy cover, perennial grass height, residual grass height, residual perennial grass canopy cover, soil nitrogen, soil inorganic carbon, soil organic carbon, and soil total carbon. We found no significant effect sizes in beetle counts or weights, soil inorganic carbon, litter, and perennial residual grass canopy cover between burned and mowed treatments. Because the previous effects were not significantly different, we did not include them in Appendices 2.B or 2.C. Effect sizes we report in the next few paragraphs were significantly different (95% confidence intervals did not overlap 0.0) and are reported in Appendices 2.B and 2.C.

Prescribed burned sites compared to mowed sites in 2008.—Ant weights (mg/trap) were 6.3-times higher at sites that were prescribed burned during the 1990s on aridic soils (effect size = 10.5, 95% CI: 1.6–19.5) and 16.9-times higher at sites that were prescribed burned on ustic soils during 2000–2006 (effect size = 77.3, 95% CI: 22.9–131.6) than mowed sites on respective soils. Beetle weights (mg/trap) were 40.6 to 85.1-times higher at sites prescribed burned on ustic soils than mowed sites on ustic soils (Appendices 2.A and 2.B). Grasshopper counts were higher at sites prescribed burned during the 1990s than mowed sites on aridic and ustic soils (Aridic soil effect size = 3.5, 95% CI: 0.8–6.2; ustic soils effect size = 3.0, 95% CI: 0.4–5.6; Appendices 2.A and 2.B). Shannon's diversity and evenness indices based on insect counts were lower for ground-dwelling insects on sites that were prescribed burned in the 1990s and during 2000–2006 than mowed sites on ustic soils (Appendices 2.A and 2.B).

Annual forbs were 6.7-times higher at sites prescribed burned during the 1990s on ustic soils than mowed sites on ustic soils (effect size = 8.7, 95% CI: 0.4–16.9). Bare ground was higher on mowed sites on aridic soils than burned sites during 1990s and during 2000–2006 on aridic soils (Appendices 2.A and 2.B). Non-sage-grouse food forbs were 15.1-times higher at sites prescribed burned during 2000–2006 on aridic soils than mowed sites on aridic soils (effect size = 8.1, 95% CI: 0.7–15.5). Perennial grass canopy cover was 4.3-times higher at sites prescribed burned during 2000–2006 on aridic soils than at mowed sites on aridic soils (effect size = 40.6, 95% CI: 12.2–69.0). Sites prescribed burned during the 1990s and during 2000–2006 on aridic soils had lower sagebrush height than mowed sites on aridic soils (Appendices 2.A and 2.B).

Prescribed burned sites compared to mowed sites in 2009.—Grasshopper weights (mg/trap) were 14.4-times higher on sites prescribed burned during the 1990s on aridic soils than mowed sites on aridic soils (effect size = 119, 95% CI: 47.2–190.9; Appendices 2.A and 2.B). Shannon's diversity and evenness indices for foliage-dwelling insects (no./sweep) were lower at sites prescribed burned during both time periods than at mowed sites on both aridic and ustic soils. Shannon's diversity and Pielou's evenness indices for ground-dwelling insects (no./trap) were higher at sites prescribed burned during the 1990s on aridic soils than mowed sites on aridic soils (Appendix 2.B).

Soil characteristics showed higher total nitrogen and total carbon at sites prescribed burned during 2000–2006 than mowed sites on both aridic and ustic soils (Appendix 2.B). Organic carbon was 11.4-times higher on sites prescribed burned during 2000–2006 on aridic sites than mowed sites on aridic soils (effect size = 5.5, 95% CI: 4.9–6.1; Appendices 2.A and 2.B).

Annual brome canopy cover was 88.2-times higher at sites prescribed burned during the 1990s on aridic soils than at mowed sites on aridic soils (effect size = 46.2, 95% CI: 14.5–77.9; Appendices 2.A and 2.B). Bare ground was lower at sites prescribed burned during 2000–2006 on aridic soils compared to mowed sites on aridic soils (bare ground was 6.5-times higher at mowed sites; effect size = –32.0, 95% CI: –43.0 to –21.1). Perennial grass height was 3.6-times higher at 1990s burns on aridic soils than mowed sites on aridic soils (effect size = 40.2, 95% CI: 25.8–54.7). Residual grass height was 1.8-times higher at sites prescribed burned during the 1990s on aridic soils than mowed sites on aridic soils (effect size = 7.4, 95% CI: 1.5–13.4). Sagebrush heights and canopy cover were lower at sites prescribed burned during the 1990s and during 2000–2006 on ustic soils than mowed sites on ustic soils. Sagebrush heights were also lower at sites that were prescribed burned during the 1990s on aridic soils than mowed sites on aridic soils (effect size = –11.3, 95% CI: –2.0 to –20.6). Sage-grouse food forbs were 3.6-times higher at sites prescribed burned during the 1990s (effect size = 2.8, 95% CI: 0.2–5.4) and 21.3-times higher at sites prescribed burns during 2000–2006 (effect size = 21.8, 95% CI: 8.1–35.6) on aridic soils than mowed sites on aridic soils. Species richness of sage-grouse food forbs was 2.6-times higher at prescribed burns during the 1990s on aridic soils than mowed sites on aridic soils (effect size = 0.6, 95% CI: 0.0 to 1.1; Appendices 2.A and 2.B).

Treatment sites compared to reference sites in 2008.—Grasshopper counts were greater at prescribed burns on aridic soils and 3.5-times greater at burns during the 1990s on ustic soils (effect size = 3.1, 95% CI: 0.8–5.4) than paired reference sites (Appendices 2.A and 2.C). Perennial grass canopy cover was 1.9-times higher at sites prescribed burned during the 1990s on ustic soils than reference sites (effect size = 14.9, 95% CI: 6.0–23.9). Wyoming big sagebrush heights were lower at mowed sites on ustic soils and at all prescribed burned sites compared to reference sites. Wyoming big sagebrush canopy cover was lower at all prescribed burned sites than reference sites (Appendix 2.C).

Treatments compared to reference sites in 2009.—Ant counts were 3.5-times greater at mowed sites on ustic soils compared to reference sites (effect size = 28.1, 95% CI: 1.5–54.7; Appendices 2.A and 2.C). Evenness of foliage-dwelling insects (no./sweep) was higher at mowed sites on ustic soils (effect size = 0.6, 95% CI: 0.3–1.0) compared to reference sites. Diversity and evenness indices of ground-dwelling insects (mg/trap) were higher at sites prescribed burned during the1990s and lower at mowed sites on aridic soils compared to reference sites (Appendix 2.C).

Bare ground was lower at sites prescribed burned during 2000–2006 on aridic soils compared to reference sites (effect size = –12.4, 95% CI: –19.3 to –5.5; Appendix 2.C). Litter was 2.5-times higher at mowed sites on aridic soils compared to reference sites (effect size =

18.0, 95% CI: 3.4–32.7). Wyoming big sagebrush heights and canopy cover were higher at reference sites compared to sites burned during the 1990s and during 2000–2006 on aridic and ustic soils (Appendices 2.A and 2.C).

Linear Contrasts

Linear contrasts that were not significantly ($P > 0.008$) different between prescribed burned and mowed treatments included ant weight, beetle weight, grasshopper weight, soil inorganic carbon, food forb calcium, food forb gross energy, food forb phosphorous, residual grass height, residual perennial grass canopy cover, sage-grouse food forb species richness, and Shannon's diversity using ground-dwelling insect weights. Soil characteristics were not significantly different when examining contrasts between treatments and reference sites, as well as insect response variables, except grasshopper counts during 2008 (Appendix 2.D).

Prescribed burned sites compared to mowed sites in 2008.**—**Ant counts were higher at sites prescribed burned during 2000–2006 versus mowed sites (linear contrast $F_{1,\,11} = 14.1$, $P = 0.001$) and sites prescribed burned during the 1990s (linear contrast $F_{1,\,17} = 8.4$, $P = 0.006$). Beetle counts and Shannon's diversity of foliage-dwelling insects were higher at sites prescribed burned during 2000–2006 than mowed sites (linear contrast $F_{1,\,11} = 8.0$, $P = 0.007$, linear contrast $F_{1,\,11} = 7.6$, $P = 0.001$; Appendix 2.D). Grasshopper counts were higher at sites prescribed burned during the 1990s versus mowed sites (linear contrast $F_{1,\,16} = 17.9$, $P < 0.001$) and sites prescribed burned during 2000–2006 (linear contrast $F_{1,\,17} = 9.0$, $P = 0.005$).

Bare ground was higher at mowed sites versus prescribed burned sites on aridic soils (linear contrast $F_{1,\,11} = 15.4$, $P < 0.001$) and sites prescribed burned during 2000–2006 (linear contrast $F_{1,\,11} = 11.3$, $P = 0.002$; Appendix 2.D). Litter (linear contrast $F_{1,\,16}=10.6$, $P = 0.002$) and annual brome canopy cover (linear contrast $F_{1,\,16} = 8.3$, $P = 0.007$) were higher at mowed sites versus sites that were prescribed burned during the 1990s. Perennial grass canopy cover was higher at sites that were prescribed burned during 2000–2006 (linear contrast $F_{1, 11} = 13.3$, $P = 0.001$) than mowed sites and higher at sites prescribed burned during 2000–2006 than sites prescribed burned during the 1990s (linear contrast $F_{1, 17} = 15.9$, $P < 0.001$). Perennial grass height was higher at prescribed burned sites on aridic soils (linear contrast $F_{1, 11} = 9.34$, $P = 0.004$) and sites that were prescribed burned during the 1990s (linear contrast $F_{1,16} = 9.2$, $P = 0.004$) than mowed sites.

Prescribed burned sites versus mowed sites in 2009.—Ground-dwelling insect diversity was higher at sites prescribed burned during the 1990s (linear contrast $F_{1, 16} = 8.7$, $P = 0.005$) compared to mowed sites and sites that were prescribed burned during 2000–2006 (linear contrast $F_{1, 17} = 8.3$, $P = 0.007$; Appendix 2.D). Shannon's diversity index of foliage-dwelling insects was higher at mowed sites versus all prescribed burned sites (Appendix 2.D).

Total soil carbon and soil organic carbon were higher at prescribed burned sites on aridic soils (linear contrast $F_{1, 11} = 15.0$, $P = < 0.001$) and sites burned during 2000–2006 versus mowed sites (linear contrast $F_{1, 11} = 28.7$, $P < 0.001$) and sites that were prescribed burned during the 1990s (linear contrast $F_{1, 17} = 18.0$, $P < 0.001$; Appendix 2.D). Soil nitrogen was higher at sites that were prescribed burned during 2000–2006 compared to mowed sites (linear contrast $F_{1, 11} = 28.3$, $P = 0.001$) and sites prescribed burned during the 1990s (linear contrast $F_{1, 17} = 18.0$, $P < 0.001$). Soil nitrogen was also higher at prescribed burned sites on aridic soils compared to mowed sites on aridic soils (linear contrast $F_{1, 11} = 13.9$, $P < 0.001$; Appendix 2.D).

Annual brome canopy cover was higher at sites prescribed burned during the 1990s versus mowed sites (linear contrast $F_{1, 16} = 8.6$, $P = 0.006$; Appendix 2.D). Sagebrush canopy cover was higher at mowed sites versus all prescribed burns except those on ustic soils

(Appendix 2.D). Sagebrush heights were higher at mowed sites versus sites that were prescribed burned during 2000–2006 (linear contrast $F_{1, 11} = 8.6$, $P = 0.006$). Perennial grass canopy cover was higher at sites that were prescribed burned during 2000–2006 versus mowed sites (linear contrast $F_{1, 11} = 8.0$, $P = 0.007$). Perennial grass height was higher sites that were prescribed burned during the 1990s and during 2000–2006 on aridic soils (linear contrast $F_{1, 11} = 9.9$, $P = 0.003$) and sites that were prescribed burned on aridic and ustic soils during 2000–2006 (linear contrast $F_{1, 11} = 9.4$, $P = 0.004$) compared to mowed sites.

Treatment sites compared to reference sites in 2008.— Grasshopper counts (no./sweep) were higher at treatment sites compared to reference sites in 2008 (linear contrast $F_{1, 48} = 8.13$, $P = 0.007$). Reference sites had higher sagebrush height (linear contrast $F_{1, 48} = 41.1$, $P < 0.001$) and canopy cover (linear contrast $F_{1, 48} = 63.5$, $P < 0.001$) in contrast to all treatments in 2008 (Appendix 2.D).

Treatment sites compared to reference sites in 2009.—Perennial grass canopy cover was higher at treatment sites when contrasted with reference sites (linear contrast $F_{1, 48} = 10.2$, $P = 0.003$). Reference sites had higher sagebrush heights (linear contrast $F_{1, 48} = 90.6$, $P < 0.001$) and canopy cover (linear contrast $F_{1, 48} = 46.8$, $P < 0.001$) than treatment sites (Appendix 2.D).

Principal Components Analysis

2008 field season.—The first 3 eigenvalues in our PCA analysis were greater than 1 and accounted for 69.4% of the total variation explained by the variables in the 2008 PCA. The first axis had the largest eigenvalue (3.243) accounting for 32.4% of the total variation, followed by the second axis (eigenvalue = 2.060; 20.6% of variation), and the third axis (eigenvalue = 1.633; 16.3% of variation).

Soil characteristics, total carbon (*r* = 0.46), and total nitrogen (*r* = 0.46) had high loadings on the first PC axis (Table 2.3, Fig. 2.4). Total carbon was over 5-times and total nitrogen was over 4-times higher, respectively, on sites that were prescribed burned during 2000–2006 on aridic soils than sites mowed on aridic soils (Appendix 2.A). Annual brome canopy cover (*r* = –0.45), Wyoming big sagebrush height (*r* = 0.45), and Wyoming big sagebrush canopy cover (*r* = 0.50) had high loadings on the second PC axis (Table 2.3; Fig. 2.4). Prescribed burned sites on aridic soils during the 1990s had high percentage of annual brome canopy cover (mean = 47.3, SE = 9.3) while sites mowed on aridic soils had fairly high annual brome canopy cover (mean = 13.4, SE = 12.9). Mowed sites had higher sagebrush heights than all prescribed burns sites on ustic soils (Appendix 2.A).

2009 field season.—The first 3 eigenvalues in our PCA analysis were greater than 1 and accounted for 76.9% of the total variation explained by the variables in the 2009 PCA. The first axis had the largest eigenvalue (3.942) accounting for 39.4% of the total variation, followed by the second axis (eigenvalue = 2.103; 21.0% of variation), and the third axis (eigenvalue = 1.645; 16.5% of variation).

Soil characteristics, total carbon (*r* = 0.48) and total nitrogen (*r* = 0.48), had high loadings on the first PC axis (Table 2.4, Fig. 2.5). Wyoming big sagebrush characteristics, height (*r* = 0.60), and canopy cover (*r* = 0.63), had high loadings on the second PC axis (Table 2.4, Fig. 2.5). Mowed sites had higher sagebrush heights than sites prescribed burned during the 1990s and during 2000–2006 on ustic soils as well as sites burned during the 1990s on aridic soils (Appendix 2.A). Wyoming big sagebrush canopy cover was higher at mowed sites on ustic soils than sites burned during the 1990s and during 2000–2006 on ustic soils (Appendix 2.A).

DISCUSSION

Our approach of comparing prescribed burning and mowing treatments in the Bighorn Basin met our objectives of evaluating differences in structural and functional response variables known to be important for sage-grouse reproduction and survival as well as ecological function. Within the time frame of the study, mowing did not provide an overall higher level of insect, soil, or vegetation responses that reflect ecological function and ecological parameters that influence sage-grouse reproduction and survival during nesting and brood-rearing than areas that were prescribed burned. When examining both mowing and prescribed burning, we found that treated sites (either prescribed burned or mowed) had lower levels of shrub structural components than reference sites, but higher levels at mowed sites compared to prescribed burned sites. Even though structural features at mowed sites were maintained, the overall enhancement of habitat characteristics important to sage-grouse nesting and brood rearing was minimal when comparing response variables to paired reference sites.

Insects

Insects important to juvenile and adult sage-grouse diets include ants, beetles, and grasshoppers (Patterson 1952, Klebenow and Gray 1958, Johnson and Boyce 1990, Connelly et al. 2000). Sage-grouse chicks require insect protein for survival until at least 3 weeks of age and are dependent on insects after 3 weeks of age to maintain normal growth rates (Johnson and Boyce 1990). In addition, the diet of adult birds in summer is dominated by forbs and insects (Patterson 1952, Wallestad and Eng 1975). Consequently, estimating the abundance and diversity of insects is fundamental to evaluating the quality of sage-grouse brood-rearing habitat.

Although abundance of beetles and ants has been found to decline following fire and mowing in mountain (Christiansen 1988) and Wyoming big sagebrush communities (Rickard 1970, Fischer et al. 1996), we found no difference between ant and beetle abundance (no./trap) when comparing prescribed burned sites to reference sites in the Bighorn Basin (Appendix 2.C). This finding is similar to a study in southeastern Idaho where beetle and ant abundance increased 1 year postburn, but returned to preburn levels 3–5 years post burn in mountain big sagebrush (Nelle at al. 2000). Two studies in Oregon found no difference in beetle abundance between burned and unburned plots in mountain big sagebrush (Pyle and Crawford 1996) or Wyoming big sagebrush (Rhodes et al. 2010). Slater (2003) reported no significant difference in insect abundance and biomass between prescribed burned and unburned sites in mountain and Wyoming sagebrush communities in southern Wyoming. Even though there was no overall significant difference between prescribed burned sites and reference sites (Appendix 2.C), we did find greater ant abundance (no./trap) at sites burned during 2000–2006 and sites burned during the 1990s on aridic soils than mowed sites (Appendix 2.B). Furthermore, ant abundance (no./trap) did not differ from paired reference sites, suggesting ant abundance was not adversely affected 2–8 years postburn in our study area. However, we did see 3.5-times greater ant abundance (no./trap) at mowed sites on ustic soils compared to reference sites (Appendix 2.C).

Fischer et al. (1996) found no difference in grasshopper abundance in Wyoming big sagebrush in southeastern Idaho among burned and unburned plots, however these authors were concerned their results were biased due to small sample size. In contrast, Rhodes et al. (2010) reported 2-times the number of grasshoppers in burned sites compared to reference sites in southeastern Oregon in Wyoming big sagebrush. In our study, we found greater grasshopper abundance (no./trap) at sites prescribed burned during the 1990s and during 2000–2006 on aridic soils than at reference sites and greater abundance of grasshoppers in 1990s burns compared to mowed sites during the 2008 field season (Appendix 2.B and Appendix 2.C). However, this difference was not seen during the 2009 field season. We attribute this inconsistency in grasshopper abundance to the 2009 field season having a higher diversity in ground dwelling insects at prescribed burned sites. Insect abundance and diversity was found to increase with higher forb cover in Gunnison sage-grouse (*C. minimus*) habitat in southeastern Utah (Ward 2007) and in lesser prairie chicken (*Tympanuchus pallidicinctus*) habitats in Kansas (Jamison et al. 2002). We may have found an increase in insect diversity during the 2009 field season due to higher forb cover on aridic soils.

Christiansen (1988) found mowed sites in mountain big sagebrush communities had lower species diversity for ants and lower species diversity and richness for beetles following treatment in southern Wyoming. Although mowed sites had higher insect diversity than prescribed burned sites in our study, mowing did not enhance diversity when compared to paired reference sites in Wyoming big sagebrush communities. Our findings are similar to Lockwood et al.'s (1990) research in southeast Wyoming, which reported no increase in insect species richness following mowing treatments in Wyoming big sagebrush.

Soil Quality

Healthy soil is the foundation of stable, productive terrestrial ecosystems. Soil provides habitat for many terrestrial organisms, including plant roots, and is the site of a number of critically important ecosystem functions such as nutrient cycling and energy transfer (Killham 1994, Coleman and Crossley 1996). One of the most crucial challenges of degraded ecosystem restoration is to reestablish healthy productive soils (Munshower 1994, Doran et al. 1996, Harris et al. 1996). Rangeland forage production and wildlife habitat are dependent on the general productivity and quality of soils (National Research Council 1994, Karlen 1997).

Soil characteristics such as total nitrogen, total carbon, and inorganic carbon were 2- to 5-times higher at prescribed burned sites than mowed sites, but these soil characteristics showed no measurable increase when comparing treatment to reference sites. Similar to our results, Davies et al. (2007) reported no difference in total carbon or total nitrogen between treatment and reference sites. Furthermore, sage-grouse food forb nutritional quality may not have been enhanced due to the lack of soil productivity following treatment. We believe our results suggest that mowing did not sufficiently disturb belowground components to elicit a measurable difference in soil nutrients. At high temperatures (i.e., >500°C) nitrogen is prone to volatilization, resulting in large loss of nutrients to the atmosphere (Neary et al. 1999). Prescribed burns from 2000–2006 had 2- to 5-times higher total nitrogen than mowed sites (Appendix 2.A), suggesting these prescribed burns did not reach temperatures that would result in a significant nitrogen loss through volatilization (Neary et al. 1999).

Vegetation

Sage-grouse are known to prefer areas with higher sagebrush canopy cover, taller grasses for nesting, and higher herbaceous canopy cover for brood-rearing throughout their range (Wallestad and Pyrah 1974, Gregg et al. 1994, DeLong et al. 1995, Connelly et al. 2000, Holloran et al. 2005, Hagen et al. 2007). Sagebrush height was 2.2- to 3.0-times higher at mowed sites on aridic soils than prescribed burned sites on aridic soils and 1.0- to 10.4-times higher at mowed sites on ustic soils than sites that were prescribed burned on ustic soils. Across treatment combinations, sagebrush canopy cover was 3.6- to 13.2-times higher at mowed sites than prescribed burned sites (Appendix 2.A). Overall we found mowing during 2000–2006 maintained adequate sagebrush canopy cover for breeding and early brood-rearing. Prescribed burning largely eliminated canopy cover of sagebrush at our burned study sites; recovering insufficiently to meet the Connelly et al. (2000) 10–15% canopy cover guidelines for breeding habitat (nesting and early brood-rearing) in xeric sagebrush communities even 19 years following treatment. Furthermore, we found sagebrush heights and canopy cover were lower at both prescribed burned and mowed sites compared to reference sites. Researchers have documented slow recovery of Wyoming big sagebrush communities following fire (Baker *In Press*, Cooper et al. 2007, Lesica et al. 2007, and Beck et al. 2009), which can eliminate nesting, early brood-rearing, and wintering habitat for sage-grouse due to loss of sagebrush canopy (Miller and Eddleman 2001, Wambolt et al. 2002).

Forbs provide an important source of protein for juvenile sage-grouse growth and development as well as other nutrients such as calcium and phosphorus needed by pre-laying females (Klebenow and Gray 1968, Johnson and Boyce 1990, Barnett and Crawford 1994, Connelly et al. 2000). Recent work in mountain big sagebrush in south-central Utah has suggested a higher response in herbaceous components following chemical and mechanical treatments (Dahlgren et al. 2006). This study also found higher use of chemically-treated plots by sage-grouse compared to reference sites, however sage-grouse use of mechanical sites was not different from non-treated reference sites (Dahlgren et al. 2006). Summers (2005) found no difference in perennial forb cover among Wyoming big sagebrush sites in northern Utah treated with mechanical techniques compared to reference sites. Similarly, in our study, we found no difference in sage-grouse food forb canopy cover, production, or nutritional quality among mowed and reference sites.

Short-term increase in calcium and protein in forbs following prescribed burning in mountain big sagebrush has been reported in portions of Montana (Dyke and Darragh 2006) and Wyoming (Cook a et al. 2004), but no increase in the nutritional quality of sage-grouse food forbs was found following either prescribed burning or mowing in the Bighorn Basin in Wyoming big sagebrush communities. Although we found burns on sites overlying aridic soils had 2.8- to 11.0-times higher food forb canopy cover than mowed sites on aridic soils, there was no measurable postburn increase of sage-grouse food forbs compared to reference sites, which coincides with other research showing no difference among sage-grouse food forb canopy cover between prescribed burned and unburned sage-grouse habitats (Fischer et al. 1996, Nelle et al. 2000, Wambolt et al. 2001, Wrobleski and Kauffman 2003, Cooper et al. 2007, Beck et al. 2009, Rhodes et al. 2010).

Structural features of perennial grasses, such as canopy cover and height, are used by sage-grouse for protection from predators during nesting, early brood-rearing, and late brood-rearing (Gregg et al. 1994, DeLong et al. 1995, Connelly et al. 2000). Mowing Wyoming big sagebrush resulted in higher canopy cover of grasses in western Wyoming compared to reference sites (J. D. Derner, USDA Agricultural Research Service, Cheyenne, Wyoming, USA, unpublished data). In our study, perennial grass canopy cover and height were 4.3- and 3.6-times higher at prescribed burned sites on aridic soils than mowed sites. Linear contrasts showed treatment sites (mowed and prescribed burned sites combined) during the 2009 field season had higher perennial grass canopy cover than reference sites. We used effect sizes to identify where these differences occurred among the 6 treatment combinations and their paired reference sites. However, effect sizes did not support differences in perennial grass canopy cover between treated sites and paired reference sits in 2009, suggesting a pooled effect, but no discernable effect in perennial grass canopy cover within individual treatments. The only difference that we detected was during the 2008 field season, where perennial grass canopy cover was higher at sites prescribed burned during the 1990s on ustic soils than paired reference sites. Furthermore, the response in perennial grass height was not increased following prescribed burning when compared to reference sites. Herbaceous responses tend to increase following fire in the short-term (2–3 years post burn; Pyle and Crawford 1996, Davies et al. 2007, Bates et al. 2009), but long-term (≥14 years postburn) responses in perennial grasses are minimal (Beck et al. 2009). Pyle and Crawford (1996) reported rapid recovery of perennial grass cover and increased bunchgrass composition following fire in mountain big sagebrush, but cover and diversity were not different from untreated controls 2 years postburn.

Annual brome canopy cover was found to be 6.5-times higher at prescribed burned sites during the 1990s than prescribed burned sites from 2000–2006. The Bighorn Basin has been invaded by cheatgrass across an estimated >80 km^2 (Wyoming Pest Detection program 2009). The expansion of cheatgrass increases the likelihood of future fires that can lead to the loss of perennial grasses and shrubs (Knick and Rotenberry 1997, Crawford et al. 2004). A study in the southeastern portion of the Bighorn Basin reported a decline in native perennial forbs, grasses, and shrubs when annual bromes exceeded 20% canopy cover (Gasch Salava 2008). Prevéy et al. (2010) found 3–4 times more exotic herbs in plots where sagebrush was removed than in undisturbed habitats. Removal of sagebrush can increase the rate of invasion by exotic plants and managers need to be aware of possible loss of perennial grasses and native forbs when implementing sagebrush removal tactics.

Many researchers have shown a 2–14 year postburn increase in bare ground immediately following prescribed burning, indicating a loss of protective ground cover for sagebrush obligate species (Castrale 1982, Petersen and Best 1987, Beck et al. 2009). We found bare ground was 1.1- to 11.9-times higher at mowed sites on aridic soils than prescribed burned sites on aridic soils. According to research on sage-grouse nesting sites, random plots normally have higher bare ground than nest sites, indicating possible avoidance of these areas (Sveum et al. 1998, Holloran 1999, Aldridge and Boyce 2007). Because of higher bare ground, mowed areas may not be used for nesting by sage-grouse, but this has not been documented.

Some of the results from our PCA analyses suggest treatments reflected annual conditions related to weather patterns. PCA analyses for 2008 indicated that annual brome canopy cover was important in these ordinations, but in 2009 this did not stand out. More precipitation in April 2009 compared to April 2008 may have led to higher perennial grass canopy cover than in 2008. The additional rainfall in 2009 (Wyoming Agricultural Statistics 2010) may have allowed perennial grasses to out compete annual bromes.

CONCLUSIONS

Although mowing is viewed as an alternative to prescribed burning, we found mixed results in support of its use over burning sagebrush communities to elicit positive responses for sage-grouse nesting and early brood-rearing. Mowing provided 3.6- to 13.2-times higher sagebrush canopy cover on ustic soils, 2.2- to 3.0-times higher sagebrush heights on aridic and ustic soils, and 1.2- to 1.5-times higher insect diversity on ustic and aridic soils than prescribed burning. However, mowing did not promote an increase in other sage-grouse early brood-rearing needs such as the abundance of food forbs, abundance or weights of beetles and grasshoppers, or perennial grass canopy cover or height. When comparing mowed sites to reference sites, mowed sites had 2- to 2.5-times higher litter on aridic soils and 3.5- to 9.1-times higher ant weights (mg/trap) on ustic soils; these are beneficial attributes for nesting and early brood-rearing habitats, but it does not seem logical to increase litter at the expense of sagebrush cover (Appendix 2.A). Mowing had lower sagebrush heights compared to reference sites. A note of caution when using mowing treatments is the higher percentage of bare ground found on mowed sites on aridic soils (1.1- to 30.8-times higher than prescribed burned sites on aridic soils), which can potentially lead to erosion (Sherman and Buckhouse 1984, Hofmann 1991), resources for exotic plant invasion (Burke and Grime 1996, Bergquist et al. 2007), increased fire frequency (West 2000, Baker *In Press*), and lower ecosystem productivity (Watts 1998).

In some cases, prescribed burning showed positive results for sage-grouse nesting and early brood-rearing habitats compared to mowing such as 6.3- to 16.9-times greater ant weights (mg/trap; on prescribed burned sites on aridic soils during the 1990s and prescribed burned sites on ustic soils during 2000–2006, respectively), 2.3- to 85.1-times greater beetle weights (mg/trap) on ustic soils, 3.6- to 4.3-times higher perennial grass canopy cover on aridic soils, 2.6-times higher plant species richness on sites at aridic soils that were burned during 2000–2006, and 2.0- to 5.0-times higher soil nitrogen on sites burned during 2000–2006, but all of these characteristics were not found to be enhanced compared to reference sites. Studies have shown differences in response variables when monitoring vegetation characteristics 2 years postburn (McGee 1982, Hobbs and Spowart 1984), but because we examined treatments that were 3–19 years old, we believe that potential 1or 2 year post-treatment effects disappeared by the time we monitored these sites, indicating most post-treatment response levels returned to pre-treatment levels, except for sagebrush structural features. The main benefit of prescribed burning for sage-grouse nesting and early brood-rearing habitats was the increase in grasshopper abundance (no./trap) compared to reference sites (grasshopper abundance was 2.4- to 3.4-times greater at prescribed burned sites than reference sites).

Enhancement of herbaceous attributes is often cited as a principal reason for treating sagebrush (Dahlgren et al. 2006); however, comparisons between values at treatment and reference sites in our study indicated that sage-grouse food forb canopy cover and nutritional quality, and perennial grass height and canopy cover (5 of 6 cases) were not enhanced through burning or mowing. Our findings are supported by other studies showing minimal or no improvement of structural features of perennial grasses or functional features of soils and forbs following burning or mowing (Wambolt et al. 2001, Davies et al. 2007, Beck et al. 2009, Davies et al. 2009, Rhodes at al. 2010).

Prescribed fire can negatively affect sage-grouse nesting habitats due to the loss of sagebrush canopy cover and height needed for nest sites (Connelly et al. 2000, Nelle et al. 2000, Wambolt et al. 2001, Thacker 2010). As a cautionary note, prescribed burns during the 1990s showed 3.5- to 88.2-times higher annual brome canopy cover compared to mowed sites, indicating a threat to perennial grasses and shrubs by increasing fine fuel buildup that can intensify wildfire frequency (Knick and Rotenberry 1997, Crawford et al. 2004). It has been suggested that prescribed burning should only be used in higher elevations where mountain big sagebrush communities are less threatened by exotic species invasion due to more mesic conditions that are beneficial for perennial plant competition (Cook et al. 1994, Thacker 2010).

MANAGEMENT IMPLICATIONS

Our results provide important considerations for managers considering burning or mowing to enhance Wyoming big sagebrush for sage-grouse in the Bighorn Basin. Mowing retained minimum levels of sagebrush canopy cover and improved ant abundance compared to reference sites, but mowing did not improve herbaceous responses, beetle abundance, or grasshopper abundance to benefit sage-grouse nesting or early brood-rearing compared to reference sites. Mowing also did not enhance soil nutrients to promote higher levels of vegetational responses following treatment. Prescribed burning maintained perennial grass canopy cover and height, but sagebrush canopy cover and height that is needed for cover by sage-grouse was drastically reduced (–85.1 to –100% and –73.0 to –94.9%, respectively) even 19 years postburn (Appendix 2.A). Our findings strongly demonstrate that managers must consider the threats inherent in treating Wyoming big sagebrush including the loss of shrub structure and potential invasion of invasive annual grasses or other weedy species, which ultimately diminish the quality of treated habitats for sage-grouse. Cheatgrass has already invaded much of the Basin and to avoid further proliferation of cheatgrass, prescribed burning Wyoming big sagebrush is not recommended.

If sagebrush community characteristics in untreated communities do not meet the minimum Connelly et al. (2000) guidelines, managers should reconsider treatments in those areas, and instead consider other practices such as improved grazing management, controlling annual weeds, removal of fences in areas where sage-grouse strikes are known or perceived to occur, removal of raptor perches, replanting sagebrush to link fragmented sagebrush habitats, eliminating unnecessary roads or other linear features or non treatment. Contrary to preferred outcomes following treatment, the reduction of Wyoming big sagebrush canopy cover may not stimulate growth of herbaceous understory (Wambolt et al. 2001). We advise managers to use caution when implementing mowing or prescribed burning in Wyoming big sagebrush communities due to the loss of sagebrush structural features that are needed for sage-grouse nesting and early brood-rearing habitats. Although our findings are specific to the Bighorn Basin of north-central Wyoming, we believe they are relevant to other ecologically similar Wyoming big sagebrush habitats where prescribed burning and mowing are planned or have been used to manage nesting and brood-rearing habitats for sage-grouse.

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Table 2.1. Functional and structural ecological response variables collected at treated and untreated sites in Wyoming big sagebrush to evaluate quality of nesting and brood-rearing habitats for greater sage-grouse, Bighorn Basin, Wyoming, 2008 and 2009.

Study component	Response variables
FUNCTION	
Ecological status	Annual brome canopy cover (%)
	Annual forb canopy cover (%)
	Bare soil (%)
	Biological soil crust ground cover (%)
	Cactus canopy cover (%)
	Perennial grass canopy cover (%)
	Perennial non-food forb canopy cover (%)
	Perennial residual grass canopy cover (%)
	Rabbitbrush canopy cover (%)
	Rock ground cover (%)
Forage availability	Food forb canopy cover (%)
	Food forb species richness (*n*)
	Food forb standing crop (kg/ha)
	Insect abundance (no./trap, no./sweep or abundance index)
	Insect biomass (mg/trap or mg/sweep by taxonomic group)
	Insect diversity (Shannon's diversity index)
	Insect evenness (Pielou's evenness index)

Table 2.1. Continued.

Study component	Response variables
Forage quality	Food forb calcium (%)
	Food forb gross energy (kcal/kg DM)
	Food forb phosphorous (%)
	Food forb protein (%)
Soil quality	Inorganic carbon (%)
	Organic carbon (%)
	Total carbon (%)
	Nitrogen (%)
	$NO3^{-}$ (mgN/kg soil)
	$NH4^{+}$ (mgN/kg soil)
Vegetation Structure	
Nesting cover	Litter (%)
	Perennial grass canopy cover (%)
	Perennial grass height (cm)
Shrub structure	Total shrub elliptical area (cm^2)
	Wyoming big sagebrush canopy cover (%)
	Wyoming big sagebrush height (cm)

Table 2.2. Perennial forbs used by greater sage-grouse and found within the Bighorn Basin, Wyoming. This list was consulted when estimating canopy cover for food and non-food forbs.

Common name	Scientific name	Status
Agoseris	*Agoseris* spp.	*Native*
Alfalfa	*Medicago sativa*	*Introduced*
Aster	*Aster* spp.	*Native*
Balsamroot	*Balsamorhiza* spp.	*Native*
Broomrape	*Orobanche* spp.	*Native*
Buckwheat	*Eriogonum* spp.	*Native*
Burningbush	*Bassia scoparia*	*Introduced*
Clover	*Trifolium* spp.	*Native/introduced*
Common pepperweed	*Lepidium densiflorum*	*Native*
Common dandelion	*Taraxacum officinale*	*Introduced*
Curlycup gumweed	*Grindelia squarrosa*	*Native*
Deathcamas	*Zigadenus*	*Native*
Desert parsley/biscuitroot	*Lomatium* spp.	*Native*
Flax	*Linum* spp.	*Native/introduced*
Fleabane	*Erigeron* spp.	*Native*
Fringed sagewort	*Artemisia frigida*	*Native*
Globemallow	*Sphaeralcea* spp.	*Native*
Goatsbeard	*Tragopogon* spp.	*Introduced*
Hawksbeard	*Crepis* spp.	*Native*

Table 2.2. Continued.

Common name	Scientific name	Status
Indian paintbrush	*Castilleja* spp.	*Native*
Lupine	*Lupinus* spp.	*Native*
Microseris	*Microseris* spp.	*Native*
Microsteris	*Microsteris gracilis*	*Native*
Milkvetch	*Astragalus* spp.	*Native*
Monkey flower	*Mimulus ringens*	*Native*
Northern sweetvetch	*Hedysarum boreale*	*Native*
Onion	*Allium* spp.	*Native*
Penstemon	*Penstemon* spp.	*Native*
Phlox	*Phlox* spp.	*Native*
Prickly lettuce	*Lactuca serriola*	*Introduced*
Prairie clover	*Dalea* spp.	*Native*
Pussytoes	*Antennaria* spp.	*Native*
Sainfoin	*Onobrychis viciifolia*	*Introduced*
Sego lily	*Calochortus nuttallii*	*Native*
Shooting stars	*Dodecatheon* spp.	*Native*
Small burnet	*Sanguisorba minor*	*Introduced*
Sweetclover	*Melilotus officinalis*	*Introduced*
Vetch	*Vicia* spp.	*Native/introduced*
Yarrow	*Achillea* spp.	*Native*

Table 2.3. Pearson's correlation coefficients for habitat variables at prescribed burned and mowed sites with 3 principal component axes, Bighorn Basin, Wyoming, USA, data collected in 2008.

2008 Habitat variables	PC1	PC2	PC3
Shrub characteristics			
Wyoming big sagebrush height (cm)	–0.22	0.45*	0.28
Wyoming big sagebrush canopy cover (%)	–0.24	0.50*	0.24
Herbaceous components			
Perennial grass canopy cover (%)	0.35	0.15	–0.11
Perennial grass height (cm)	0.28	0.09	0.57*
Annual brome canopy cover (%)	0.01	–0.45*	0.10
Ground cover			
Litter (%)	–0.25	0.01	–0.59*
Bare ground (%)	–0.42	0.06	0.10
Soil Characteristics			
Total nitrogen (%)	0.46*	0.27	–0.18
Total carbon (%)	0.46*	0.28	–0.19
Insect characteristics			
Grasshopper (no./sweep)	0.19	–0.41	0.32

*Correlation coefficients $r \geq 0.45$ indicating habitat predictor variables highly correlated with respective principal component axes.

Table 2.4. Pearson's correlation coefficients for habitat variables at prescribed burned and mowed sites with 3 principal component axes, Bighorn Basin, Wyoming, USA, data collected in 2009.

2009 Habitat variables	PC1	PC2	PC3
Shrub characteristics			
Wyoming big sagebrush height (cm)	–0.04	0.60*	0.28
Wyoming big sagebrush canopy cover (%)	–0.12	0.63*	0.09
Herbaceous components			
Perennial grass canopy cover (%)	0.35	–0.22	–0.13
Perennial grass height (cm)	0.37	0.16	0.27
Annual brome canopy cover (%)	–0.07	–0.22	0.62*
Food forb (%)	0.37	0.26	–0.04
Ground cover			
Litter (%)	–0.07	–0.15	0.54*
Bare ground (%)	–0.34	0.16	–0.37
Soil Characteristics			
Total nitrogen (%)	0.48*	0.05	–0.05
Total carbon (%)	0.48*	0.04	–0.07

*Correlation coefficients $r \geq 0.45$ indicating habitat variables highly correlated with respective principal component axes.

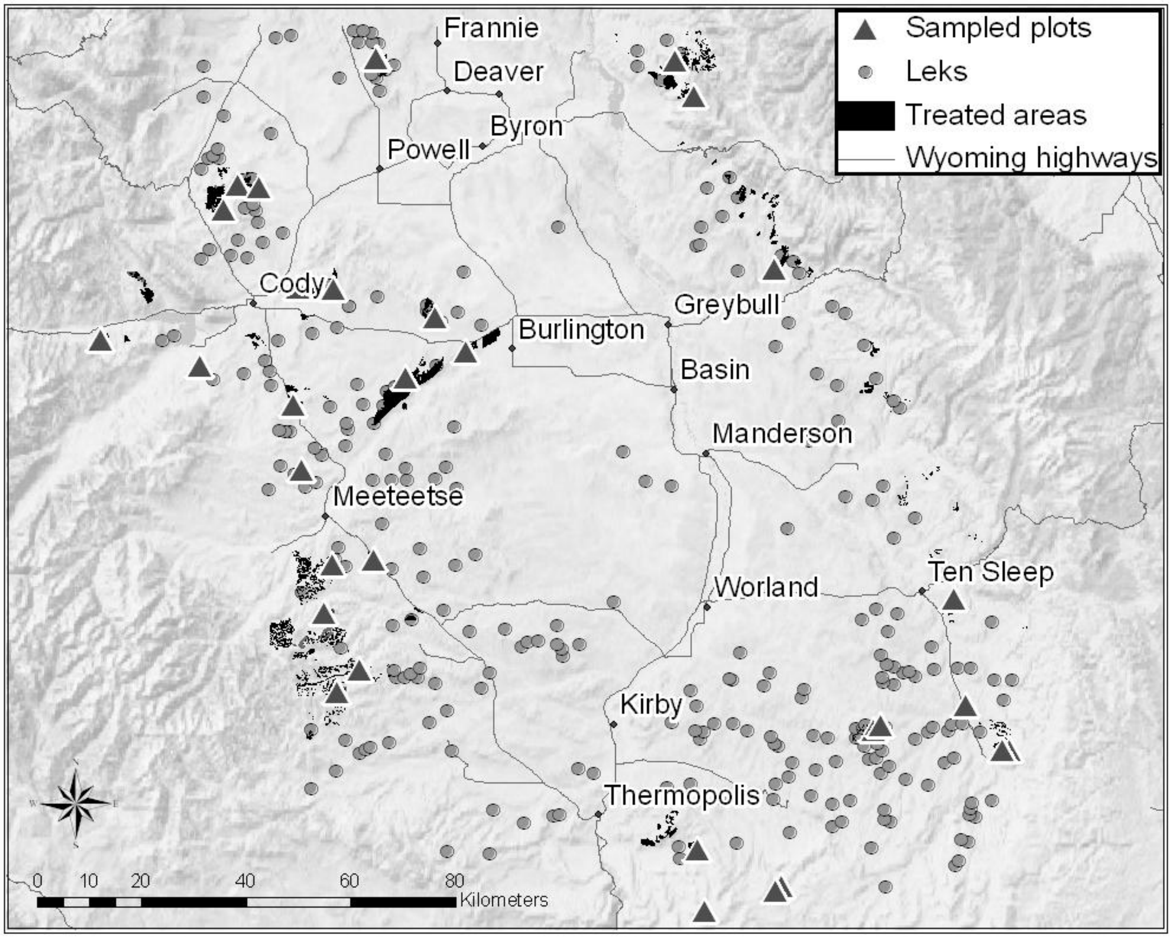

Figure 2.1. Greater sage-grouse leks in relation to prescribed burned and mowed sampled sites in the Bighorn Basin, Wyoming, USA, 2008 and 2009. The average distance from sampled site to lek was 4.5 km (range: 0.2–11.8 km).

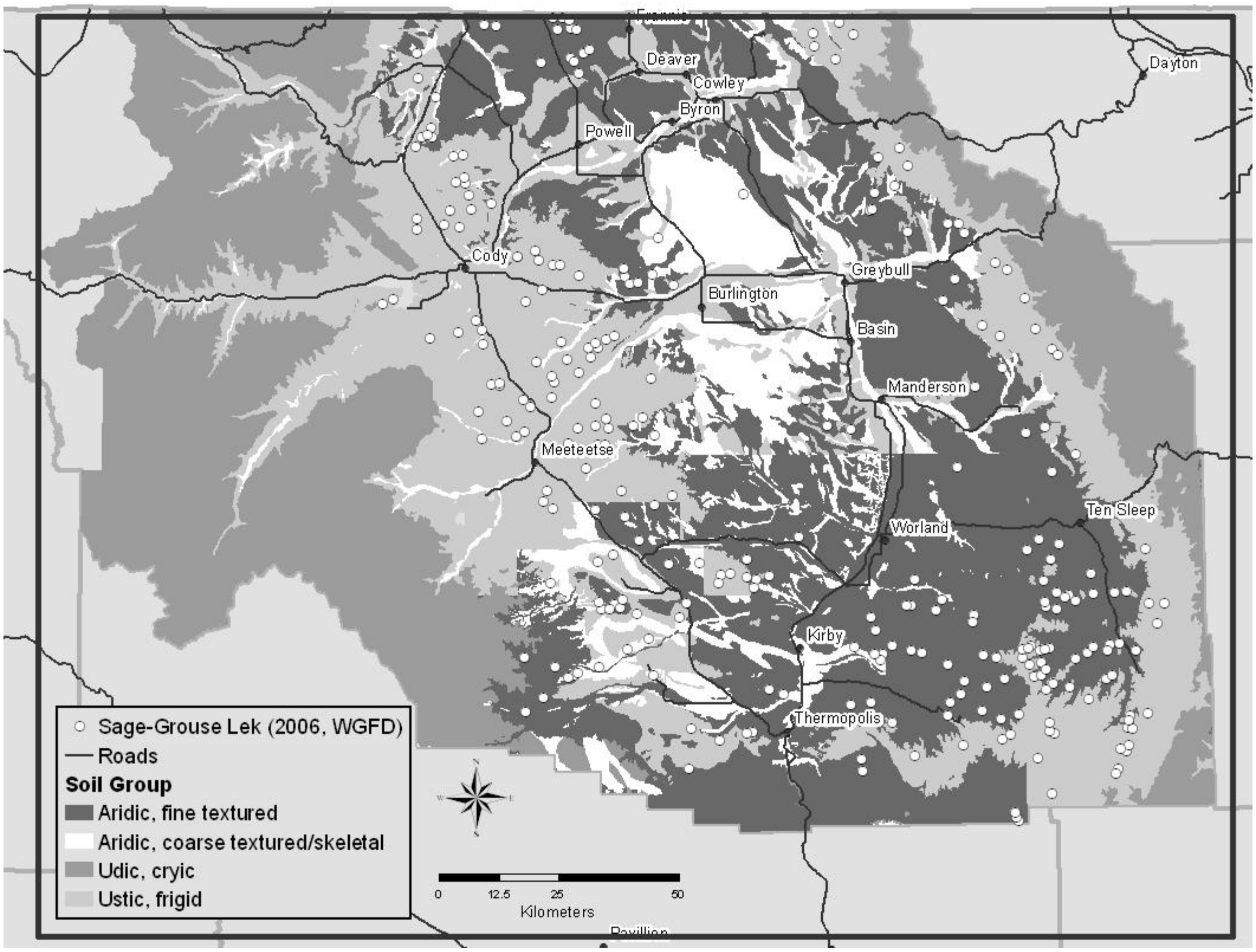

Figure 2.2. Greater sage-grouse lek sites overlying the distribution of major soil groupings in the Bighorn Basin, Wyoming, USA. Soil groupings were based on soil temperature, moisture, and texture, which largely influence establishment and development of sagebrush communities in the Bighorn Basin. Geographic data provided by Bill Wilson, GIS Specialist, Bureau of Land Management, Cody, Wyoming and NRCS SSURGO soils database (http://soils.usda.gov/survey/geography/ssurgo/).

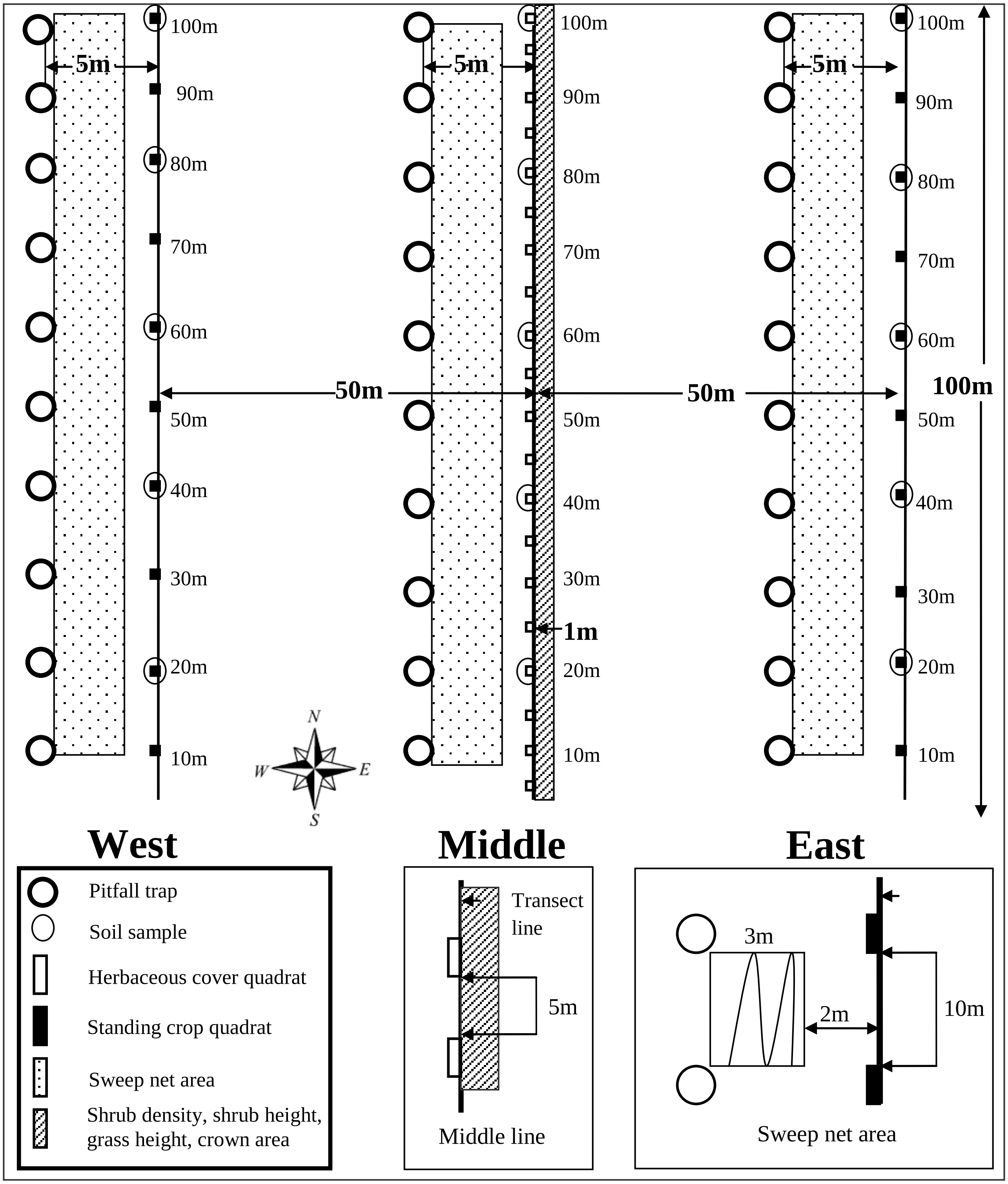

Figure 2.3. Schematic representation of 3, 100-m x 1-m transects (i.e., west, middle, and east) for comparing mowed and prescribed burned sites in the Bighorn Basin, Wyoming USA, 2008 and 2009.

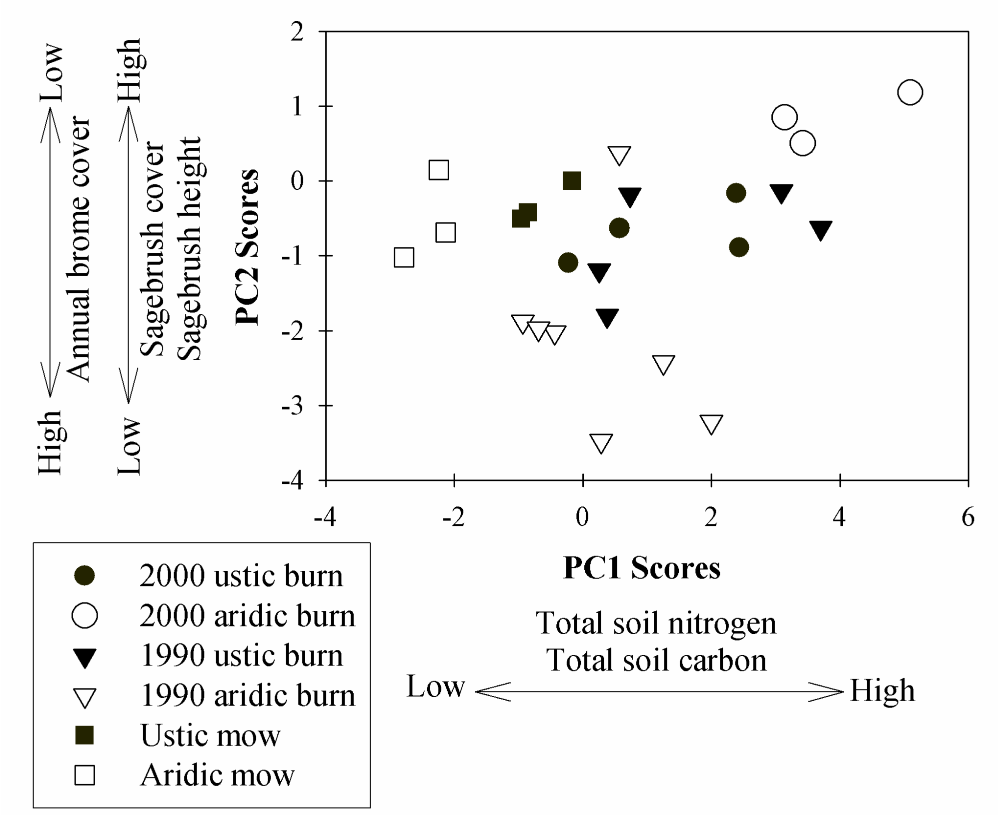

Figure 2.4. Ordination of principal components scores for prescribed burned (during 1990s and during 2000–2006) and mowed sites (during 2000–2006) along the first 2 principal component axes, Bighorn Basin, Wyoming, USA, 2008. Aridic and ustic refer to different general soil groupings where aridic are fine-textured soils in more arid climates and ustic are soils with intermediate soil moisture in cool temperature regimes.

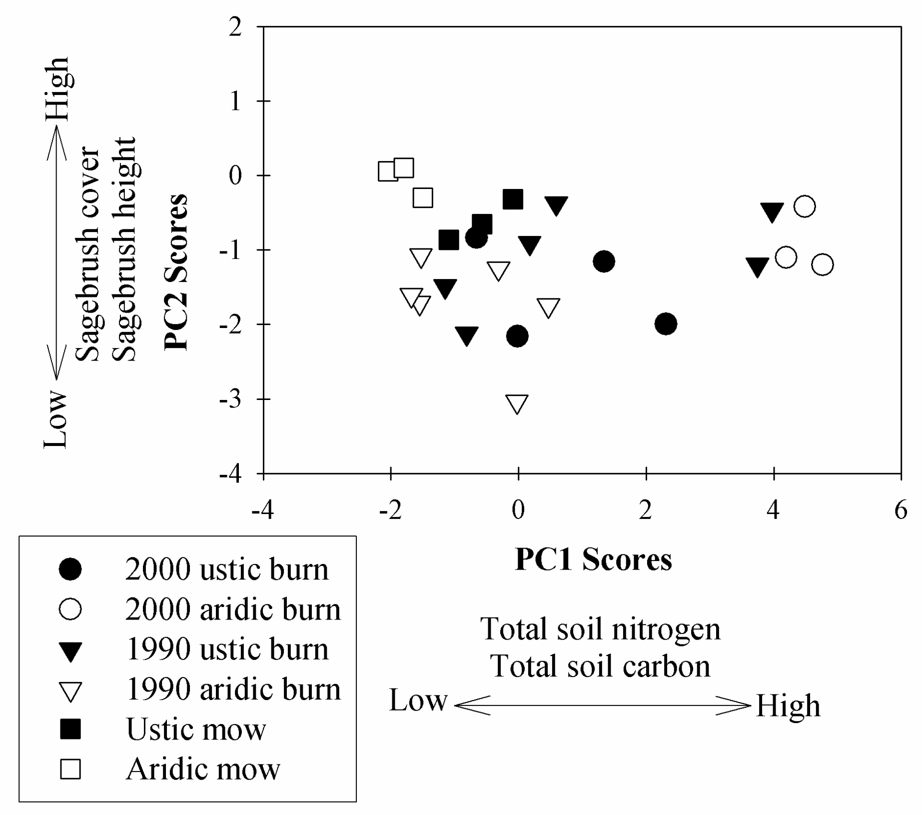

Figure 2.5. Ordination of principal components scores for prescribed burned (during 1990s and during 2000–2006) and mowed sites (during 2000–2006) along the first 2 principal component axes, Bighorn Basin, Wyoming, USA, 2009. Aridic and ustic refer to different general soil groupings where aridic are fine-textured soils in more arid climates and ustic are soils with intermediate soil moisture in cool temperature regimes.

APPENDIX 2.A. Mean (± SE) of response variables at prescribed burned, mowed, and paired reference sites in the Bighorn Basin, Wyoming, USA, 2008 and 2009. Combination refers to treatment combinations; for example, 1990 aridic refers to sites prescribed burned during the 1990s on aridic soils. Aridic and ustic refer to different general soil groupings where aridic are fine-textured soils in more arid climates and ustic are soils with intermediate soil moisture in cool-temperature regimes.

Insect Characteristics		Ants (mg/trap)		Ant (no./trap)		Beetle (mg/trap)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	12.5 ± 3.7	11.6 ± 4.0	2.5 ± 0.3	2.9 ± 0.9	132.0 ± 64.8	101.3 ± 43.5
	2009	44 ± 30.7	55.7 ± 23	4.3 ± 1.7	8.3 ± 3.8	147.5 ± 56	98.1 ± 29.4
1990 ustic	2008	173.8 ± 91.1	343.2 ± 299.0	23.1 ± 10.6	5.8 ± 1.7	255.3 ± 64.6	390.6 ± 156.4
	2009	1416.7 ± 1214.4	99.2 ± 71.3	18.4 ± 9.9	10.4 ± 4.8	351 ± 247.5	174.2 ± 57.1
2000 aridic	2008	428.2 ± 203.6	299.3 ± 244.7	54.0 ± 19.2	41.1 ± 19.0	338.8 ± 187.4	627.4 ± 190.7
	2009	541.8 ± 326.1	475.4 ± 371	58.2 ± 29.1	41.4 ± 29	146.3 ± 69.2	171.7 ± 24.6
2000 ustic	2008	82.1 ± 21.0	193.0 ± 114.0	14.6 ± 3.8	25 ± 9.5	121.9 ± 41.6	215.2 ± 71.7
	2009	10467.1 ± 10427.6	7716.7 ± 7329.5	11.9 ± 5	11.4 ± 8.3	382.3 ± 345.2	643.2 ± 459.1
Mow aridic	2008	2 ± 0.5	0.4 ± 0.3	1.4 ± 0.2	1.1 ± 0.1	2 ± 0.7	6.4 ± 2.0
	2009	242.9 ± 211.5	26.7 ± 16.6	20.7 ± 17.2	4.5 ± 1.3	212.7 ± 60	200.9 ± 20.6
Mow ustic	2008	4.9 ± 2.6	1.4 ± 0.9	2.1 ± 0.3	1.2 ± 0.3	3 ± 1.1	2.5 ± 1.4
	2009	250.4 ± 81.3	60.5 ± 21.7	39.2 ± 7.8	11.1 ± 2.9	108.2 ± 45.7	171.9 ± 76.3

Appendix 2.A. Continued.

Combination	Year	Beetle (no./trap)		Grasshopper (mg/sweep)		Grasshopper (no./sweep)		Pitfall Shannon's Diversity[a]	
		Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	1.3 ± 0.3	1.3 ± 0.2	222.2 ± 56.7	64.6 ± 22.9	4.3 ± 1.0	1.4 ± 0.3	1.4 ± 0.1	1.5 ± 0.1
	2009	0.7 ± 0.2	0.9 ± 0.1	127.9 ± 30.2	52.4 ± 28.9	6.2 ± 2.4	2.1 ± 0.6	1.6 ± 0.1	1.3 ± 0.1
1990 ustic	2008	2.5 ± 0.9	1.2 ± 0.3	299.6 ± 81.7	130.1 ± 35.9	4.4 ± 1.0	1.3 ± 0.2	1.2 ± 0.2	1.3 ± 0.2
	2009	1 ± 0.1	0.8 ± 0.2	66.5 ± 22.8	29.6 ± 5	3.8 ± 1.2	1.6 ± 0.5	1.1 ± 0.2	1.2 ± 0.2
2000 aridic	2008	5.5 ± 3.2	3.2 ± 0.5	226.2 ± 177.9	78.9 ± 75.1	1.5 ± 0	0.2 ± 0.1	0.9 ± 0.2	1.2 ± 0.3
	2009	1.7 ± 0.3	1.5 ± 0.5	76.9 ± 21.3	73.7 ± 53.8	1.1 ± 0.3	1.5 ± 0.4	0.7 ± 0.3	0.8 ± 0.2
2000 ustic	2008	2.0 ± 0.6	2.0 ± 0.6	609.6 ± 379.3	324.4 ± 169.8	2.8 ± 0.8	2.1 ± 0.7	1.1 ± 0.1	0.9 ± 0.1
	2009	1.3 ± 0.4	0.7 ± 0.4	412.9 ± 382.5	43.9 ± 15.8	2.7 ± 1.2	4.6 ± 2.4	0.9 ± 0.1	0.8 ± 0.2
Mow aridic	2008	0.8 ± 0.2	1.0 ± 0.5	40.9 ± 36.8	35.6 ± 33.7	0.9 ± 0.6	0.7 ± 0.5	1.7 ± 0.1	1.7 ± 0
	2009	1.2 ± 0.2	1.4 ± 0.2	8.9 ± 3	21.9 ± 17.8	1.2 ± 0.3	1.5 ± 0.6	0.5 ± 0.1	1 ± 0.1
Mow ustic	2008	1.4 ± 0.4	1.3 ± 0.4	134.1 ± 114.7	47.4 ± 37.3	1.4 ± 0.4	1.8 ± 1.1	1.7 ± 0	1.7 ± 0.1
	2009	1 ± 0.3	1.2 ± 0.2	44.4 ± 26.6	218.6 ± 206.6	2 ± 0.1	1.7 ± 0.6	1.1 ± 0.3	1.3 ± 0.1

Appendix 2.A. Continued.

Combination	Year	Pitfall Shannon's Diversity[b]		Sweep net Pielou's evenness[c]		Sweep net Pielou's evenness[d]		Sweep net Shannon's Diversity[c]	
		Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	0.8 ± 0.2	1.1 ± 0.2	0.5 ± 0.1	0.7 ± 0.0	0.5 ± 0.0	0.4 ± 0.1	1.1 ± 0.1	1.4 ± 0.1
	2009	1.1 ± 0.1	1.1 ± 0.2	0.4 ± 0.1	0.6 ± 0.1	0.7 ± 0.0	0.8 ± 0	1.4 ± 0.1	1.6 ± 0.1
1990 ustic	2008	1.1 ± 0	1 ± 0.1	0.6 ± 0.0	0.6 ± 0.0	0.5 ± 0.1	0.6 ± 0.1	1.2 ± 0.1	1.3 ± 0.0
	2009	1.1 ± 0.2	1 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.7 ± 0.0	0.8 ± 0.0	1.4 ± 0.4	1.6 ± 0.1
2000 aridic	2008	1.4 ± 0.1	1 ± 0.4	0.6 ± 0.1	0.5 ± 0.2	0.6 ± 0.1	0.4 ± 0.2	1.2 ± 0.2	1.1 ± 0.4
	2009	1.1 ± 0.3	1 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0	0.8 ± 0.0	1.4 ± 0.1	1.5 ± 0.1
2000 ustic	2008	1.3 ± 0.1	1.2 ± 0	0.6 ± 0.1	0.6 ± 0.0	0.6 ± 0.2	0.6 ± 0.2	1.2 ± 0.1	1.2 ± 0.1
	2009	1.2 ± 0.2	1 ± 0.2	0.8 ± 0	0.6 ± 0.1	0.6 ± 0.1	0.7 ± 0	1.3 ± 0.2	1.4 ± 0.0
Mow aridic	2008	1.2 ± 0.3	1 ± 0.4	0.7 ± 0	0.7 ± 0.1	0.3 ± 0.2	0.4 ± 0.3	1.5 ± 0.1	1.5 ± 0.2
	2009	0.8 ± 0.2	1.1 ± 0.3	0.8 ± 0.1	0.6 ± 0.1	0.9 ± 0	0.9 ± 0	1.7 ± 0.0	1.7 ± 0.1
Mow ustic	2008	1.5 ± 0.1	1.2 ± 0.2	0.7 ± 0	0.8 ± 0	0.2 ± 0.1	0.6 ± 0	1.5 ± 0.1	1.6 ± 0.1
	2009	1 ± 0.1	0.9 ± 0.1	0.6 ± 0.2	0.5 ± 0.2	1.5 ± 0.1	0.9 ± 0	1.7 ± 0.1	1.7 ± 0.0

Appendix 2.A. Continued.

Soil Characteristics		$NH4^+$ (mgN/kg soil)		$NO3^-$ (mgN/kg soil)		Total carbon (%)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	—[e]	—	—	—	—	—
	2009	3.0 ± 0.3	2.7 ± 0.3	1.8 ± 0.6	1.1 ± 0.5	1.3 ± 0.3	1 ± 0.2
1990 ustic	2008	—	—	—	—	—	—
	2009	4.6 ± 0.5	3.5 ± 0.9	3.9 ± 1.0	3.4 ± 1.9	2.8 ± 0.8	2.5 ± 0.7
2000 aridic	2008	—	—	—	—	—	—
	2009	13.0 ± 3.4	9.0 ± 4.6	8.3 ± 6.8	5.5 ± 4.8	6.3 ± 0.1	3.1 ± 1.1
2000 ustic	2008	—	—	—	—	—	—
	2009	8.6 ± 1.8	3.4 ± 0.3	5.3 ± 1.5	2.7 ± 1.0	2.4 ± 0.3	1.9 ± 0.4
Mow aridic	2008	—	—	—	—	—	—
	2009	3.6 ± 0.8	2.7 ± 0.5	2.7 ± 0.4	1.3 ± 0.6	0.8 ± 0.1	0.8 ± 0.2
Mow ustic	2008	—	—	—	—	—	—
	2009	3.3 ± 0.5	2.6 ± 0.1	1.2 ± 0.5	0.8 ± 0.5	1.1 ± 0.3	1.2 ± 0.4

Appendix 2.A. Continued.

		Total inorganic carbon (%)		Total nitrogen (%)		Total organic carbon (%)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	—	—	—	—	—	—
	2009	0.3 ± 0.1	0.3 ± 0.1	0.1 ± 0	0.1 ± 0	1 ± 0.3	0.8 ± 0.2
1990 ustic	2008	—	—	—	—	—	—
	2009	0.4 ± 0.1	0.3 ± 0	0.2 ± 0.1	0.2 ± 0.1	2.4 ± 0.8	2.3 ± 0.7
2000 aridic	2008	—	—	—	—	—	—
	2009	0.3 ± 0.1	0.1 ± 0	0.5 ± 0	0.3 ± 0.1	6 ± 0.1	3.1 ± 1
2000 ustic	2008	—	—	—	—	—	—
	2009	0.4 ± 0.1	0.5 ± 0.3	0.2 ± 0	0.2 ± 0	1.9 ± 0.3	1.4 ± 0.2
Mow aridic	2008	—	—	—	—	—	—
	2009	0.3 ± 0.2	0.3 ± 0	0.1 ± 0	0.1 ± 0	0.5 ± 0.1	0.5 ± 0.2
Mow ustic	2008	—	—	—	—	—	—
	2009	0.1 ± 0	0.4 ± 0.2	0.1 ± 0	0.1 ± 0	1 ± 0.3	0.8 ± 0.4

Appendix 2.A. Continued.

Vegetation Characteristics		Annual brome (%)		Annual forb (%)		Bare ground (%)		Biological soil crust (%)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	47.3 ± 9.3	23.2 ± 9.3	7.1 ± 3	5 ± 2.7	17.8 ± 6.4	31.1 ± 7.3	2.2 ± 1	1.4 ± 0.5
	2009	46.7 ± 13.4	41.9 ± 12.4	4.3 ± 0.7	8.1 ± 4.2	24.8 ± 8.4	33.6 ± 7.6	0.6 ± 0.1	0.7 ± 0.1
1990 ustic	2008	4.3 ± 2.4	1.3 ± 0.5	10.2 ± 3.4	3.2 ± 1.2	25.4 ± 6.6	34 ± 9.7	1 ± 0.3	0.9 ± 0.2
	2009	4.1 ± 3.2	2.7 ± 2.1	10 ± 4.4	3 ± 1.1	27.2 ± 6	32.4 ± 7.4	0.5 ± 0	0.7 ± 0.1
2000 aridic	2008	6.3 ± 1	8.8 ± 4.2	9 ± 4.3	4.8 ± 3.5	4.4 ± 1.4	1.7 ± 2.1	0.8 ± 0.2	0.8 ± 0.2
	2009	9.5 ± 4.6	8.1 ± 3.8	3.6 ± 2.2	4.3 ± 3	5.8 ± 0.5	18.2 ± 2.1	0.5 ± 0	0.5 ± 0
2000 ustic	2008	2.3 ± 1.2	1.4 ± 0.9	11.9 ± 10.4	3.5 ± 1.7	21.1 ± 5.5	25.7 ± 4.7	11.8 ± 6.2	7.6 ± 4.1
	2009	3.3 ± 2.7	1.8 ± 1.2	10.4 ± 6.1	4.8 ± 2.2	23.9 ± 3.3	38.2 ± 6.3	10.5 ± 6.2	9.3 ± 5.1
Mow aridic	2008	13.4 ± 12.9	2 ± 1.5	4.9 ± 2.7	0.6 ± 0.1	52.5 ± 7.2	56.9 ± 14.3	1.3 ± 0.4	1 ± 0.4
	2009	0.5 ± 0	0.5 ± 0	2.3 ± 0.8	1.7 ± 0.7	37.8 ± 3.4	50.2 ± 17.4	0.5 ± 0	0.8 ± 0.2
Mow ustic	2008	0.6 ± 0.1	0.6 ± 0.1	1.5 ± 0.6	2.5 ± 1.7	31.6 ± 3.1	27.7 ± 2.9	1.1 ± 0.3	2.5 ± 1.1
	2009	0.9 ± 0.4	0.8 ± 0.2	4.7 ± 3.1	3.8 ± 1.5	20.8 ± 1.3	30.4 ± 8.2	0.6 ± 0.1	0.8 ± 0.2

Appendix 2.A. Continued.

		Cactus canopy cover (%)		Food forb cover (%)		Food forb calcium (%)		Food forb gross energy (kcal/kg DM)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	1.6 ± 0.6	1.1 ± 0.3	3.1 ± 1.4	2.9 ± 1.7	1.5 ± 0.5	1.2 ± 0.6	4300.0 ± 82.6	4216.0 ± 64.6
	2009	1.9 ± 0.7	0.9 ± 0.2	3.9 ± 1	5.5 ± 3.2	1.2 ± 0.3	1.6 ± 0.7	4596.0 ± 110.5	4362.8 ± 85.1
1990 ustic	2008	1.1 ± 0.5	0.6 ± 0	9.8 ± 5	16.8 ± 7.7	1.4 ± 0.4	2 ± 0.5	4515.6 ± 105.3	4270.8 ± 94.9
	2009	0.6 ± 0	0.7 ± 0.1	17.7 ± 8	25.4 ± 9.9	1.1 ± 0.2	1.7 ± 0.2	4546.8 ± 72.4	4436.7 ± 64
2000 aridic	2008	0.5 ± 0	0.5 ± 0	12.1 ± 4.1	6.2 ± 1.1	1.8 ± 0.7	2.2 ± 1	4547.5 ± 81.5	4296.3 ± 102.8
	2009	0.5 ± 0	0.5 ± 0	22.9 ± 4.3	13.7 ± 4.8	2.5 ± 0.5	2.3 ± 0.5	4495 ± 156	4404 ± 61.8
2000 ustic	2008	1.3 ± 0.8	0.7 ± 0.2	4.8 ± 2.4	3.7 ± 1	1.2 ± 0.4	1.4 ± 0.2	4453.8 ± 29.4	4542 ± 92.7
	2009	0.6 ± 0	1 ± 0.5	7.4 ± 2.5	8.3 ± 2.1	1.3 ± 0.3	1.4 ± 0.3	4487.4 ± 81.1	4560.1 ± 144.8
Mow aridic	2008	1.9 ± 0.8	0.9 ± 0.2	0.6 ± 0.1	1.8 ± 0.8	1.1 ± 0	1.4 ± 0.1	—[f]	—
	2009	0.9 ± 0.2	0.8 ± 0.3	1.1 ± 0.5	4.1 ± 2.6	1.7 ± 0.4	1.7 ± 0.6	4417.7 ± 178	4486.0 ± 195.5
Mow ustic	2008	2.4 ± 1.3	1.6 ± 1	0.9 ± 0.2	3.4 ± 1.7	0.8 ± 0.5	1.2 ± 0.6	4318.0 ± 0	4475.0 ± 0
	2009	3.9 ± 1.3	0.5 ± 0	2 ± 0.7	7.2 ± 2.8	1.8 ± 0	1.7 ± 0.4	4064.0 ± 0	4479.8 ± 218.3

Appendix 2.A. Continued.

		Food forb phosphorus (%)		Food forb protein (%)		Food forb species richness (*n*)		Food forb standing crop (kg/ha)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	0.3 ± 0.1	0.2 ± 0.1	10.5 ± 3	7.5 ± 3	0.3 ± 0.1	0.5 ± 0.2	1 ± 0.8	0.4 ± 0.3
	2009	0.3 ± 0.1	0.2 ± 0.1	9.3 ± 3.6	7.3 ± 2.3	0.5 ± 0.1	0.4 ± 0.1	0.8 ± 0.4	0.6 ± 0.5
1990 ustic	2008	0.3 ± 0	0.3 ± 0	15.5 ± 1.1	14 ± 0.6	1.1 ± 0.4	1.7 ± 0.6	1 ± 0.5	2.8 ± 2.2
	2009	0.3 ± 0	0.2 ± 0	13.6 ± 2.1	12.8 ± 1.2	1.4 ± 0.5	1.6 ± 0.5	1.8 ± 1	2.4 ± 1.7
2000 aridic	2008	0.4 ± 0.2	0.3 ± 0.1	19.3 ± 5.7	16.2 ± 4	0.5 ± 0.1	0.5 ± 0.3	2.8 ± 0.1	1.5 ± 0
	2009	0.3 ± 0	0.2 ± 0.1	12.1 ± 0.6	14 ± 0	0.9 ± 0.1	0.7 ± 0.1	2.6 ± 0.3	2.3 ± 0
2000 ustic	2008	0.3 ± 0	0.3 ± 0	16.7 ± 0.7	17.3 ± 2.1	1 ± 0.2	1.1 ± 0.3	0.5 ± 0.3	0.3 ± 0.1
	2009	0.5 ± 0.3	0.3 ± 0	16 ± 2.3	16.7 ± 2.1	0.7 ± 0.1	0.8 ± 0.1	0.4 ± 0.2	0.5 ± 0.1
Mow aridic	2008	0.2 ± 0.1	0.2 ± 0.1	15.2 ± 9	9.8 ± 6.4	0.2 ± 0.1	0.2 ± 0.1	0 ± 0	0 ± 0
	2009	0.3 ± 0	0.3 ± 0.1	15.1 ± 3.4	11.3 ± 2.2	0.4 ± 0.1	0.7 ± 0.3	0.1 ± 0.1	0.2 ± 0.1
Mow ustic	2008	0.2 ± 0.1	0.2 ± 0.1	9.4 ± 5	13.1 ± 3.7	0.4 ± 0.1	0.3 ± 0.1	0 ± 0	0 ± 0
	2009	0.3 ± 0.1	0.3 ± 0	3.3 ± 5	12.1 ± 3.2	0.4 ± 0.2	0.6 ± 0.1	0.1 ± 0.1	0.5 ± 0.1

Appendix 2.A. Continued.

Combination	Year	Litter (%)		Non food forb (%)		Perennial grass canopy cover (%)		Perennial grass height (cm)	
		Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	13.3 ± 3.3	15.4 ± 3.3	0.8 ± 0.1	0.7 ± 0.1	14.2 ± 5.4	15.1 ± 3.8	31.3 ± 6.9	37.8 ± 6.1
	2009	30.9 ± 3.6	32.4 ± 3.6	1.9 ± 1.4	0.8 ± 0.2	29.8 ± 5.6	20.2 ± 1.7	25.5 ± 4.6	29.3 ± 4.3
1990 ustic	2008	10.4 ± 1.4	14.2 ± 2.5	1.9 ± 0.9	2.6 ± 1	31.3 ± 3.7	16.4 ± 1.7	42.5 ± 5.7	44.8 ± 6.3
	2009	24.4 ± 2.8	23.6 ± 3.4	2.9 ± 1.8	2.4 ± 1.2	47.1 ± 4.4	32.4 ± 3.3	27.6 ± 4.7	34.1 ± 5.9
2000 aridic	2008	18.3 ± 6.3	21.6 ± 4.3	8.7 ± 2.3	6.1 ± 2.4	53 ± 8	26.2 ± 12.5	33.7 ± 15.1	30.8 ± 13.2
	2009	18.8 ± 0.5	24.8 ± 3	5.7 ± 2	6 ± 4.4	48.3 ± 4.8	27.5 ± 7.8	55.5 ± 4.2	49.2 ± 2.8
2000 ustic	2008	16.6 ± 4.5	12.5 ± 1.9	0.7 ± 0.1	0.5 ± 0	40 ± 11.7	34.4 ± 3.3	36.6 ± 8.2	30.6 ± 5.1
	2009	22.6 ± 2.7	22 ± 2.7	3.7 ± 1.8	2.1 ± 1.6	51.3 ± 12.6	40.8 ± 8.8	26.8 ± 6.4	27.8 ± 7.5
Mow aridic	2008	29.3 ± 11.8	19.3 ± 7.5	0.6 ± 0.1	8.1 ± 2.3	12.4 ± 3.9	14.2 ± 6.3	16.0 ± 5.5	23.9 ± 0.2
	2009	29.8 ± 3.5	11.7 ± 3	0.5 ± 0	0.5 ± 0	22.1 ± 5.8	14.9 ± 6	15.3 ± 1.7	13.5 ± 3.9
Mow ustic	2008	23.6 ± 6.3	19.8 ± 4.1	1.1 ± 0.3	1.4 ± 0.4	30 ± 9.8	30 ± 4	26.5 ± 9	23 ± 4.8
	2009	28.4 ± 4.6	21.2 ± 3.9	0.5 ± 0	0.5 ± 0	37.8 ± 3.4	29.5 ± 5.8	26.5 ± 9.6	26 ± 8.8

Appendix 2.A. Continued.

		Rabbitbrush canopy cover (%)		Residual grass canopy cover (%)		Residual grass height (cm)		Rock (%)	
Combination	Year	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	0 ± 0	0 ± 0	2.4 ± 1.6	2.8 ± 1.8	17 ± 3.6	21.3 ± 2.8	1.8 ± 1	4.9 ± 5.1
	2009	0.1 ± 0.1	0.2 ± 0.2	9.5 ± 4.2	5.1 ± 1.3	16.7 ± 2.4	17.8 ± 1.3	2.4 ± 1.3	6.2 ± 4.2
1990 ustic	2008	0.2 ± 0.2	0.1 ± 0.1	1.8 ± 0.9	1.4 ± 0.4	16.5 ± 2.9	17.7 ± 3.3	2.7 ± 2.6	6.2 ± 3.3
	2009	0.5 ± 0.4	0 ± 0	5.8 ± 2.5	5 ± 2.4	13.7 ± 4.4	17.5 ± 3.8	4.4 ± 3.4	9 ± 5.9
2000 aridic	2008	0 ± 0	0.1 ± 0.1	5.7 ± 3.7	5.3 ± 2.6	33.2 ± 6.3	28.5 ± 5.8	1.2 ± 0.7	10.5 ± 2.3
	2009	0.2 ± 0.2	0.1 ± 0.1	2.7 ± 1.5	4.1 ± 0.8	25.2 ± 6	21.5 ± 2.9	0.5 ± 0	15.5 ± 3.2
2000 ustic	2008	0 ± 0	0.1 ± 0.1	6 ± 2.4	3.1 ± 1.4	17.8 ± 3.7	21.4 ± 5.4	1.3 ± 0.3	1.2 ± 0.3
	2009	0 ± 0	0 ± 0	5.6 ± 4.4	2.7 ± 0.4	15.3 ± 3.3	14.7 ± 3	1.4 ± 0.8	2.2 ± 0.8
Mow aridic	2008	0 ± 0	0 ± 0	3.4 ± 1.9	2.1 ± 0.8	16 ± 5.5	28.6 ± 4.2	1 ± 0.1	11.4 ± 6.5
	2009	0.1 ± 0.1	0.1 ± 0.1	5.4 ± 1.7	4.1 ± 2	9.3 ± 0.6	8.3 ± 1.7	1.7 ± 0.5	26.5 ± 4.6
Mow ustic	2008	0 ± 0	0.1 ± 0.1	5.4 ± 1.7	8.9 ± 3.5	16.6 ± 8.2	24.5 ± 6.7	0.8 ± 0.1	13.1 ± 9.9
	2009	0 ± 0	0 ± 0	13.2 ± 1.3	7.5 ± 1.4	11.5 ± 1.7	13.2 ± 0.5	1.5 ± 0.2	14 ± 8.2

Appendix 2.A. Continued.

Combination	Year	Total shrub elliptical area (cm2)		Wyoming big sagebrush canopy cover (%)		Wyoming big sagebrush height (cm)	
		Treatment	Reference	Treatment	Reference	Treatment	Reference
1990 aridic	2008	512.4 ± 320.4	1558.9 ± 275.3	1.6 ± 1.4	14.7 ± 3.8	8.3 ± 5	36.9 ± 5.8
	2009	953.3 ± 271.5	4281.9 ± 474.8	2 ± 0.9	13.4 ± 1.9	9.6 ± 2.8	35.6 ± 2.7
1990 ustic	2008	317.1 ± 252.6	1989.5 ± 280.6	0.9 ± 0.7	20.6 ± 2.3	10.1 ± 4.5	51.2 ± 5.8
	2009	1112.8 ± 528.9	5505.1 ± 1192.7	2.3 ± 1.3	20.4 ± 2.6	8.3 ± 2.5	40.3 ± 5.7
2000 aridic	2008	55.6 ± 55.6	2879.5 ± 102.6	0 ± 0	17.4 ± 4.5	2.4 ± 2.4	45.1 ± 3.4
	2009	239.8 ± 216.5	15805.5 ± 1577.2	0.4 ± 0.4	14.9 ± 1.3	5.4 ± 4.3	52 ± 4.5
2000 ustic	2008	64.7 ± 44.3	1679.4 ± 121.5	0.1 ± 0.1	21.5 ± 3.2	1.8 ± 1.3	35.5 ± 4.2
	2009	972.2 ± 599.5	4390.3 ± 751	1.3 ± 0.8	13.3 ± 4.2	5.9 ± 3.4	35 ± 3.9
Mow aridic	2008	795.2 ± 112.3	1383.9 ± 688.9	6.7 ± 2.4	13 ± 6.5	24.9 ± 4.8	31.6 ± 5.9
	2009	1644 ± 76.6	3634.7 ± 2080.7	11.8 ± 5.8	15.2 ± 3.5	20.9 ± 2.7	24.1 ± 8.8
Mow ustic	2008	524.4 ± 266	1221.8 ± 289.8	5.3 ± 2.9	11.3 ± 3.7	15.8 ± 1.7	29.8 ± 3.8
	2009	2315.5 ± 746.3	0.4 ± 0.1	8.2 ± 1.4	12.7 ± 3.1	18.8 ± 1.9	28.7 ± 5.2

[a] Calculated using no./trap.

[b]Calculated using mg/trap.

[c]Calculated using no./sweep.

[d]Calculated using mg/sweep.

[e]Field sampling of soils conducted in 2009.

[f]Not enough sample for analysis.

APPENDIX 2.B. Effect sizes for 1990s and 2000s prescribed burned sites compared to sites mowed during 2000–2006.

Effect sizes, standard errors (SE), and 95% confidence intervals (CI) for mean insect, soil, and vegetation response variables between prescribed burned sites in the 1990s and during 2000–2006 compared to sites mowed during 2000–2006, Bighorn Basin, Wyoming, USA. We collected these data during the 2008 and 2009 field seasons. Effect sizes with confidence intervals including zeros were not statistically different in mean reponse after burning compared to the mean response following mowing. Only significant effect sizes are presented (CIs do not overlap 0). Treatment combinations are based on decade of treatment and soil type. Aridic and ustic refer to different general soil groupings where aridic are fine-textured soils in more arid climates and ustic are soils with intermediate soil moisture in cool-temperature regimes.

						95% CI	
Habitat variable	Year	Soil	Effect	Effect size	SE	Lower	Upper
Insect characteristics							
Ants (mg/trap)	2008	Aridic	1990 burn – mow	10.5	3.8	1.61	19.48
		Ustic	2000 burn – mow	77.3	21.1	22.94	131.60
Ants (no./trap)	2008	Aridic	1990 burn – mow	1.1	0.3	0.33	1.90
		Ustic	2000 burn – mow	12.5	3.8	2.61	22.36
Beetle (mg/trap	2008	Ustic	1990 burn – mow	252.3	64.6	405.01	99.51

Appendix 2.B. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	Upper
		Ustic	2000 burn – mow	118.9	41.6	225.88	11.95
Grasshoppers (no./sweep)	2008	Aridic	1990 burn – mow	3.5	1.1	0.75	6.16
		Ustic	1990 burn – mow	3.0	1.1	0.42	5.58
Grasshoppers (mg/sweep)	2009	Aridic	1990 burn – mow	119.0	30.4	47.19	190.86
Pitfall Shannon's diversity[a]	2008	Ustic	1990 burn – mow	–0.6	0.2	–1.11	–0.06
		Ustic	2000 burn – mow	–0.6	0.1	–0.97	–0.26
	2009	Aridic	1990 burn – mow	1.1	0.2	0.68	1.49
Pitfall Pielou's evenness[a]	2008	Ustic	1990 burn – mow	–0.3	0.1	–0.57	0.03
		Ustic	2000 burn – mow	–0.3	0.1	–0.50	–0.13
Pitfall Shannon's diversity[b]	2008	Ustic	1990 burn – mow	–0.4	0.1	–0.72	–0.12
Pitfall Pielou's evenness[b]	2008	Ustic	1990 burn – mow	–0.2	0.1	–0.37	–0.06
Sweep net Shannon's diversity[c]	2009	Aridic	1990 burn – mow	–0.4	0.1	–0.61	–0.16

Appendix 2.B. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	Upper
		Aridic	2000 burn – mow	–0.3	0.1	–0.51	–0.10
		Ustic	1990 burn – mow	–0.3	0.1	–0.44	–0.07
Sweep net Pielou's evenness[c]	2009	Aridic	1990 burn – mow	–0.2	0.08	–0.3	–0.1
		Aridic	2000 burn – mow	–0.2	0.05	–0.31	–0.08
		Ustic	1990 burn – mow	–0.8	0.1	–1.08	–0.48
		Ustic	2000 burn – mow	–0.9	0.2	–1.37	–0.38
Sweep net Shannon's diversity[d]	2009	Aridic	1990 burn – mow	–0.7	0.2	–1.20	–0.19
Sweep net Pielou's evenness[d]	2009	Aridic	1990 burn – mow	–0.4	0.1	–0.62	–0.10
Soil Characteristics							
Organic carbon (%)	2009	Aridic	2000 burn – mow	5.5	0.2	4.89	6.06
Total carbon (%)	2009	Aridic	2000 burn – mow	5.4	0.4	5.11	5.76
		Ustic	2000 burn – mow	1.3	0.0[e]	1.22	1.32
Total nitrogen (%)	2009	Aridic	2000 burn – mow	0.4	0.0[e]	0.38	0.48
		Ustic	2000 burn – mow	0.1	0.0[e]	0.00[e]	0.21

Appendix 2.B. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	95%CI Upper
Vegetation characteristics							
Annual brome canopy cover (%)	2009	Aridic	1990 burn – mow	46.2	13.4	14.46	77.95
Annual forb (%)	2008	Ustic	1990 burn – mow	8.7	3.5	0.45	16.95
Bare ground (%)	2008	Aridic	1990 burn – mow	–34.7	9.6	–57.48	–11.95
		Aridic	2000 burn – mow	–48.1	7.3	–71.33	–24.80
	2009	Aridic	2000 burn – mow	–32.0	3.5	–43.02	–21.06
Food forb canopy cover (%)	2009	Aridic	1990 burn – mow	2.8	1.1	0.23	5.45
		Aridic	2000 burn – mow	21.8	4.3	8.05	35.61
Non-food forb canopy cover (%)	2008	Aridic	2000 burn – mow	8.1	2.3	0.73	15.50
Perennial grass canopy cover (%)	2008	Aridic	2000 burn – mow	40.6	8.9	12.15	69.00
Perennial grass height (cm)	2009	Aridic	2000 burn – mow	40.2	4.5	25.79	54.65
Perennial residual grass canopy cover (%)	2009	Aridic	1990 burn – mow	–7.4	2.8	–14.0	–0.8
Residual grass height (cm)	2009	Aridic	1990 burn – mow	7.4	2.5	1.46	13.38
Species richness (no./0.1 m^2)	2008	Ustic	2000 burn – mow	0.6	0.2	0.12	1.05

Appendix 2.B. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	Upper
	2009	Aridic	1990 burn – mow	0.6	0.2	0.01	1.05
Wyoming big sagebrush canopy cover (%)	2009	Ustic	1990 burn – mow	–5.9	1.9	–10.41	–1.45
		Ustic	2000 burn – mow	–6.9	1.6	–11.92	–2.96
Wyoming big sagebrush height (cm)	2008	Aridic	1990 burn – mow	–16.6	6.9	–32.90	–0.38
		Aridic	2000 burn – mow	–22.5	5.3	–39.49	–5.46
		Ustic	2000 burn – mow	–13.9	2.1	–19.40	–8.49
	2009	Aridic	1990 burn – mow	–11.3	3.9	–20.60	–2.99
		Ustic	1990 burn – mow	–10.5	3.2	–17.93	–3.02
		Ustic	2000 burn – mow	–12.9	3.9	–25.38	–0.47

[a]Calculated using no./trap.

[b]Calculated using mg/trap.

[c]Calculated using no./sweep.

[d]Calculated using mg/sweep.

[e]Values are above 0.0, but the true number is not shown because it is lower than 2 decimal places.

APPENDIX 2.C. Effect sizes for 1990s and 2000s prescribed burned sites and sites mowed during 2000–2006 compared to untreated reference sites.

Effect sizes**,** standard errors (SE), and 95% confidence intervals (CI) in mean insect, soil, and vegetation response variables between prescribed burned sites in the 1990s and during 2000–2006 and sites mowed during 2000–2006 compared to untreated reference sites (i.e., treatment mean – reference mean), Bighorn Basin, Wyoming, USA, 2008 and 2009. Effect sizes with confidence intervals including zeros are not statistically different in mean burn reponse compared to mean response at untreated reference sites or mean mow response compared to mean response at untreated reference sites. Only significant effect sizes are presented (CIs do not overlap 0). Treatment combinations are based on decade of treatment and soil type.

							95%CI	
	Habitat variable	Year	Soil	Effect	Effect size	SE	Lower	Upper
Insect characteristics								
	Ants (no./trap)	2009	Ustic	Mow – reference	28.1	8.4	1.50	54.67
	Grasshoppers (mg/sweep)	2008	Aridic	1990 burn – reference	157.6	61.8	21.32	293.93
	Grasshoppers (no./sweep)	2008	Aridic	1990 burn – reference	2.9	1.0	0.58	5.24
			Aridic	2000 burn – reference	1.3	0.1	0.92	1.63
			Ustic	1990 burn – reference	3.1	1.0	0.81	5.44

Appendix 2.C. Continued.

	Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	Upper
	Pitfall Shannon's diversity[a]	2009	Aridic	1990 burn – reference	0.3	0.1	0.00[c]	0.64
	Pitfall Pielou's evenness[a]	2009	Aridic	1990 burn – reference	0.2	0.1	0.00[c]	0.33
			Aridic	Mow – reference	–0.3	0.1	–0.53	0.01
	Sweep net Pielou's evenness[b]	2009	Ustic	Mow – reference	0.6	0.1	0.26	1.04
Vegetation characteristics								
	Bare ground (%)	2009	Aridic	2000 burn – reference	–12.4	2.2	–19.3	–5.5
	Litter (%)	2009	Aridic	Mow – reference	18.0	4.6	3.41	32.67
	Perennial grass canopy cover (%)	2008	Ustic	1990 burn – reference	14.9	4.0	5.97	23.92
	Wyoming big sagebrush canopy cover (%)	2008	Aridic	1990 burn – reference	–13.1	4.1	–22.18	–4.01
			Aridic	2000 burn – reference	–17.3	4.5	–31.71	–2.93
			Ustic	1990 burn – reference	–19.8	2.4	–25.02	–14.53

Appendix 2.C. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	95%CI Upper
		Ustic	2000 burn – reference	–21.4	3.2	–29.21	–13.60
	2009	Aridic	1990 burn – reference	–11.4	2.1	–16.07	–6.80
		Aridic	2000 burn – reference	–14.5	1.3	–18.76	–10.27
		Ustic	1990 burn – reference	–18.1	3.0	–24.71	–11.55
		Ustic	2000 burn – reference	–12.1	4.2	–22.44	–1.71
Wyoming big sagebrush height (cm)	2008	Aridic	1990 burn – reference	–28.7	7.6	–45.62	–11.69
		Aridic	2000 burn – reference	–42.7	4.2	–55.98	–29.38
		Ustic	1990 burn – reference	–33.2	12.6	–61.34	–5.07
		Ustic	2000 burn – reference	–33.6	4.4	–44.33	–22.91
		Ustic	Mow – reference	–14.0	4.2	–27.38	–0.66
	2009	Aridic	1990 burn – reference	–26.0	3.9	–34.68	–17.32
		Aridic	2000 burn – reference	–46.7	6.2	–66.28	–27.03

Appendix 2.C. Continued.

Habitat variable	Year	Soil	Effect	Effect size	SE	95%CI Lower	95%CI Upper
		Ustic	1990 burn – reference	–32.0	6.2	–45.82	–18.22
		Ustic	2000 burn – reference	–29.1	5.2	–41.83	–16.36

[a] calculated using mg/trap
[b] calculated using no./sweep
[c] Values are above 0.0, but the true number is not shown because it is lower than 2 decimal places

APPENDIX 2.D. Linear contrasts for 1990s and 2000s prescribed burned sites, sites mowed during 2000–2006, and untreated reference sites. Summary of significant ($P < 0.008$; Bonferroni correction) linear contrasts among insect, soil, and vegetation response variables between prescribed burned, mowed and reference sites, Bighorn Basin, Wyoming, USA, 2008 and 2009. Contrasts included (1) treatment compared to reference sites, (2) prescribed burns during the 1990s compared to prescribed burns during 2000–2006, (3) mowed sites compared to prescribed burns during the 1990s, (4) mowed sites compared to prescribed burns during 2000–2006, (5) mowed sites compared to prescribed burned sites on aridic soils, and (6) mowed sites compared to prescribed burned sites on ustic soils. Aridic and ustic refer to different general soil groupings where aridic are fine-textured soils in more arid climates and ustic are soils with intermediate soil moisture in cool temperature regimes. Mean (± SE) follow order of variables; for example, in 2008, beetles (no./pitfall trap) at mowed sites (mean = 1.1, SE = 0.2) and at 2000 prescribed burned sites (mean = 3.5, SE = 1.4).

Habitat variable	Year	Contrast	F_{df}	P	Mean ± SE	Mean ± SE
Insect characteristics						
Beetles (no./ trap)	2008	Mow v. 2000 burns	$8.04_{1, 11}$	0.007	1.1 ± 0.2	3.5 ± 1.4
Ants (no./ trap)	2008	Mow v. 2000 burns	$14.14_{1, 11}$	0.001	1.7 ± 0.2	31.5 ± 11.0
		1990 burns v. 2000 burns	$8.39_{1, 17}$	0.006	12.8 ± 5.9	31.5 ± 11.0
Grasshoppers (no./sweep)	2008	Treatment v. reference	$8.13_{1, 48}$	0.007	3.0 ± 0.5	1.3 ± 0.2
		Mow v. 1990 burns	$17.91_{1, 16}$	<0.001	1.1 ± 0.3	4.4 ± 0.7

Appendix 2.D. Continued.

Habitat variable	Year	Contrast	F_{df}	*P*	Mean ± SE	Mean ± SE
		1990 burns v. 2000 burns	$8.99_{1, 17}$	0.005	4.4 ± 0.7	2.3 ± 0.5
Pitfall Shannon's index[a]	2008	Mow v. 2000 burns	$12.05_{1, 11}$	0.001	1.7 ± 0.1	1.0 ± 0.1
	2009	Mow v. 1990 burns	$8.69_{1, 16}$	0.005	0.8 ± 0.2	1.3 ± 0.1
		1990 burns v. 2000 burns	$8.26_{1, 17}$	0.007	1.3 ± 0.1	0.8 ± 0.1
Sweepnet Shannon's index[b]	2009	Mow aridic v. burn aridic	$7.97_{1, 11}$	0.008	1.8 ± 0.0	1.4 ± 0.1
		Mow ustic v. burn ustic	$8.42_{1, 12}$	0.006	1.7 ± 0.1	1.4 ± 0.1
		Mow v. 1990 burns	$12.58_{1, 16}$	0.001	1.7 ± 0.0	1.4 ± 0.1
		Mow v. 2000 burns	$13.55_{1, 11}$	0.001	1.7 ± 0.0	1.3 ± 0.1
Sweepnet Shannon's index[c]	2008	Mow v. 2000 burns	$7.63_{1, 11}$	0.009	0.5 ± 0.2	1.3 ± 0.2
Soil characteristics						
Organic carbon (%)		Mow aridic v. burn aridic	$16.02_{1, 11}$	<0.001	0.5 ± 0.1	2.7 ± 0.9
		Mow v. 2000 burns	$27.25_{1, 11}$	<0.001	0.7 ± 0.2	3.7 ± 0.8
		1990 burns v. 2000 burns	$18.12_{1, 17}$	<0.001	1.7 ± 0.5	3.7 ± 0.8
Total carbon (%)		Mow aridic v. burn aridic	$15.09_{1, 11}$	<0.001	0.8 ± 0.1	2.9 ± 0.9

Appendix 2.D. Continued.

	Habitat variable	Year	Contrast	F_{df}	P	Mean ± SE	Mean ± SE
			Mow v. 2000 burns	$28.67_{1, 11}$	<0.001	1.0 ± 0.1	2.9 ± 0.9
			1990 burns v. 2000 burns	$17.98_{1, 17}$	<0.001	2.0 ± 0.5	2.9 ± 0.9
	Total nitrogen (%)		Mow aridic v. burn aridic	$13.88_{1, 11}$	0.001	0.1 ± 0.0	0.3 ± 0.1
			Mow v. 2000 burns	$28.32_{1, 11}$	<0.001	0.1 ± 0.0	0.3 ± 0.1
			1990 burns v. 2000 burns	$18.87_{1, 17}$	<0.001	0.2 ± 0.00	0.3 ± 0.1
Vegetation							
	Annual brome canopy cover						
	(%)	2008	Mow v. 1990 burns	$8.25_{1, 16}$	0.007	7.0 ± 6.5	25.8 ± 7.9
			1990 burns v. 2000 burns	$11.77_{1, 17}$	0.002	25.8 ± 7.9	4.0 ± 1.1
		2009	Mow v. 1990 burns	$8.6_{1, 16}$	0.006	0.7 ± 0.2	25.4 ± 9.2
	Bare ground (%)	2008	Mow aridic v. burn aridic	$15.35_{1, 11}$	<0.001	52.5 ± 7.2	13.3 ± 4.7
			Mow v. 2000 burns	$11.27_{1, 11}$	0.002	42.1 ± 5.8	14.0 ± 4.5
	Crude protein (%)	2009	Mow ustic v. burn ustic	$11.18_{1, 12}$	0.002	3.3 ± 3.3	14.5 ± 1.34
	Litter (%)	2008	Mow v. 1990 burns	$10.63_{1, 16}$	0.002	26.4 ± 6.1	11.8 ± 1.8

Appendix 2.D. Continued.

Habitat variable	Year	Contrast	F_{df}	*P*	Mean ± SE	Mean ± SE
Perennial grass height (cm)	2008	Mow aridic v. burn aridic	$9.35_{1, 11}$	0.004	16.0 ± 5.5	32.1 ± 6.2
		Mow v. 1990 burns	$9.21_{1, 16}$	0.004	13.7 ± 7.0	36.9 ± 4.6
	2009	Mow aridic v. burn aridic	$9.85_{1, 11}$	0.003	15.3 ± 1.7	35.5 ± 5.9
		Mow v. 2000 burns	$9.35_{1, 11}$	0.004	20.9 ± 5.0	39.1 ± 6.9
Perennial grass canopy cover (%)	2008	Mow v. 2000 burns	$13.29_{1, 11}$	0.001	21.2 ± 6.2	45.6 ± 7.4
		1990 burns v. 2000 burns	$15.89_{1, 17}$	<0.001	22.8 ± 4.0	45.6 ± 7.4
	2009	Treatment v. reference	$10.15_{1, 48}$	0.003	39.6 ± 3.3	27.8 ± 2.5
		Mow v. 2000 burns	$8.03_{1, 11}$	0.007	29.9 ± 4.6	50.0 ± 7.0
Wyoming big sagebrush canopy cover (%)	2008	Treatment v. reference	$63.49_{1, 48}$	<0.001	2.1 ± 0.7	16.9 ± 1.6
	2009	Treatment v. reference	$46.75_{1, 48}$	<0.001	3.7 ± 0.9	15.4 ± 1.2
		Mow aridic v. burn aridic	$15.36_{1, 11}$	<0.001	11.8 ± 0.3	1.5 ± 0.7
		Mow v. 1990 burns	$27.67_{1, 16}$	<0.001	10.0 ± 1.0	2.1 ± 0.8

Appendix 2.D. Continued.

Habitat variable	Year	Contrast	F_{df}	P	Mean ± SE	Mean ± SE
		Mow v. 2000 burns	$27.17_{1, 11}$	<0.001	10.0 ± 1.0	0.9 ± 0.5
Wyoming big sagebrush						
height (cm)	2008	Treatment v. reference	$41.4_{1, 48}$	<.001	11.8 ± 3.2	39.6 ± 2.6
	2009	Treatment v. reference	$90.58_{1, 48}$	<0.001	10.7 ± 1.6	36.4 ± 2.4
		Mow v. 2000 burns	$8.6_{1, 11}$	0.006	19.9 ± 1.6	5.7 ± 2.4

[a] calculated using no./trap
[b] calculated using no./sweep
[c] calculated using mg/trap

CHAPTER 3

SYNERGISTIC INFLUENCE OF DISTURBANCE FACTORS ON GREATER SAGE-GROUSE LEK PERSISTENCE

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ABSTRACT

Detecting the disappearance of active leks is the most efficient way to determine large declines in greater sage-grouse (*Centrocercus urophasianus*) populations; thus, it is critical to understand factors that influence lek persistence. The purpose of this study was to evaluate factors that may have influenced the probability of sage-grouse lek persistence in the Bighorn Basin of north-central, Wyoming from 1980 to 2009. Our objective was to examine lek persistence based on landscape characteristics that may explain differences between occupied and unoccupied leks. We designed an evaluation to examine the individual and combined effects of anthropogenic and natural landscape characteristics to sage-grouse lek persistence. We evaluated lek persistence from 144 occupied and 39 unoccupied leks from the Wyoming Game and Fish Department lek database with sufficient data for a 30-year analysis. We conducted the analyses with binary logistic regression using landscape predictor variables obtained from geographic coverages, including sagebrush community disturbance variables (e.g., agricultural development, oil and gas development, roads, wildfire) at 6 different scales (0.8 km, 1.0 km, 1.6 km, 3.2 km, 5.0 km, and 6.4 km radii around leks) to evaluate how these disturbances have influenced lek persistence. Three of the 45 models were highly competitive ($\Delta AIC_c < 2$); these included density of oil and gas wells in a 1.0-km radius, percent area of wildfire in a 1.0-km radius, and roads in a 6.4-km radius around sage-grouse leks. Unoccupied leks had 1.1-times the percentage of road area in a

6.4-km radius; 3.1-times the percentage of wildfires in a 1.0-km radius; and 10.3-times the density of wells in a 1.0-km radius compared to occupied leks. Model-averaged estimates were used to compute odds ratios, variance decomposition values, and cross validation to evaluate goodness-of-fit. The odds of lek persistence with every 1 unit increase in oil and gas wells within a 1.0-km radius was 0.71 (95% CI: 0.50–0.99). The odds of lek persistence with every 1% increase in the area of roads in a 6.4-km radius around a lek was 0.94 (95% CI: 0.87–1.02). The odds of leks persistence with every 1% increase in wildfire in a 1.0-km radius was 0.99 (95% CI: 0.98–0.99). Because the 95% CI around the model-averaged odds ratios of wells and wildfire did not overlap 1.0, we suggest these 2 predictor variables were most influential in the model-averaged estimates. Our results show support for the synergistic influence of multiple disturbance factors influencing sage-grouse lek persistence. Because these factors are interrelated, increasing roads, energy development, and wildfire are predicted to result in loss of more sage-grouse leks in the Bighorn Basin. The Bighorn Basin has lower developed reserves of oil and gas than many other regions of Wyoming; however, our study supports findings from studies in these areas that demonstrate energy development negatively affects lek persistence. Our findings indicate conservation efforts should be focused on minimizing well development and implementing wildfire suppression tactics within 1.6-km of active sage-grouse leks.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) are the largest grouse species in North America and once occupied 1,247,004 km^2 of sagebrush habitats in 13 of the western United States and 3 Canadian provinces (Schroeder et al. 2004, Braun 2006). Sage-grouse are now found in Alberta, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, Saskatchewan, South Dakota, Utah, Washington, and Wyoming (Schroeder et al. 2004). Recent studies have indicated dramatic local and range-wide declines in leks and lek attendance (Connelly and Braun 1997, Johnson et al. 2010) with remaining populations predicted to decline on an individual basis, across management zones, and range-wide within the next 30 to 100 years (Garton et al. *In press*). The current distribution of sage-grouse represents an estimated 56% of their historical range (Schroeder et al. 2004). Sage-grouse populations have declined throughout their historical habitats through many factors related to habitat loss and fragmentation (Braun 1998, Connelly et al. 2004) including increasing natural disturbance factors such as wildfires (Connelly and Braun 1997, Connelly et al. 2000*a*, *b*) and anthropogenic disturbances to sagebrush communities including agricultural development (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005, Aldridge et al. 2008, Walker et al. 2007), historical livestock-related activities (Beck and Mitchell 2000, Crawford et al. 2004), urbanization (Braun 1987, 1998; Connelly et al. 2004), energy development (Aldridge and Boyce 2007, Walker et al. 2007, Harju et al. 2010, Doherty et al. 2010), invasion of exotic species (Connelly et al. 2000*b*), and prescribed fire (Connelly and Braun 1997, Connelly et al. 2000*a*, Nelle et al. 2000). Recently, the U.S. Fish and Wildlife Service concluded that greater sage-grouse are warranted for protection under the Endangered Species Act of 1973, but because threats are moderate in magnitude and do not occur across their range at an equal intensity, the listing is precluded to other species under severe threat of extinction (U.S. Fish and Wildlife Service 2010).

Many examples indicate that individual disturbance factors such as plowing (Swenson et al. 1987, Leonard et al. 2000), large-scale prescribed burning programs (Connelly et al. 2000*a*), and energy development (Walker et al. 2007, Doherty et al. 2010, Harju et al. 2010) lead to declines in sage-grouse populations. On the other hand, the synergistic influence of multiple factors leading to loss of sage-grouse habitats and populations has been suggested (Braun 1987, 1998), and should be the focus of future research (Johnson et al. 2010, Naugle et al. *In Press*). The cumulative effects of anthropogenic disturbance in landscapes surrounding leks were associated with declining sage-grouse population trends throughout the sage-grouse range (Johnson et al. 2010). Because no single factor has led to the decline in sage-grouse populations, examining several disturbance factors leading to habitat loss and fragmentation is noteworthy because they often influence other factors that lead to synergistic loss and fragmentation of sagebrush habitats. Roads in particular are known for fragmenting and increasing levels of human activity in sagebrush habitats (Oyler-McCance et al. 2001, Knick et al. 2003, Braun et al. 2005). Elevated human activity in sagebrush habitats can lead to higher frequencies of wildfire, which, in turn may rapidly lead to habitat loss for sage-grouse (Connelly et al. 2004). Burning increases the establishment and spread of invasive plant species such as cheatgrass (*Bromus tectorum*; Knick 1999). Cheatgrass competes with native plant species for soil water following fire and depletes it faster than in areas without cheatgrass (Melgoza et al. 1990), thus leading to a competitive advantage during the growing season. Fire frequency is increased with cheatgrass invasion; the establishment of cheatgrass causes substantial competition for resources used by native shrub-steppe species (Whisenant 1990, Knick and Rotenberry 1997). Developing roads have also been found to accelerate the dispersal and establishment of exotic plant species (Gelbard and Belnap 2003, Bergquist et al. 2007).

An index computed from the average males attending leks is the most commonly used sample statistic to monitor trends in sage-grouse populations (Beck and Braun 1980), whereas quantifying the disappearance of active leks is the most efficient way to determine large declines in populations (Connelly et al. 2004). Consequently, population-level evaluations can be conducted by comparing lek persistence (i.e., ratio of occupied to unoccupied leks in a population) to long term changes in habitat characteristics for regional populations (e.g., Smith et al. 2005, Walker et al. 2007).

Range-wide declines in grouse numbers are likely a result of numerous causative factors rather than just one (Connelly et al. 2004, Crawford et al. 2004, Johnson et al. 2010), suggesting that synergistic effects of landscape disturbances may be influencing population persistence for sage-grouse. More specifically, the indirect effects of multiple disturbances on sage-grouse habitats may be driving lek abandonment through habitat loss and fragmentation near leks (Crawford et al. 2004, Smith et al. 2005). Often researchers examine specific factors that may influence populations, but the synergy of perturbations may be far more detrimental to population persistence than the sum of their individual effects. For example, the combination of predators and pesticides was found to be 2- to-4 times more deadly to gray tree frog tadpoles (*Hyla versicolor*) than when the pesticide was applied independently (Sih et al. 2004). In an avian example, populations of the lesser prairie chicken (*Tympanuchus pallidicinctus*) have declined by more than 78% since 1960 (Crawford 1980, Taylor and Guthery 1980, Hagen and Giesen 2005) with the leading causes of decline being a combination of anthropogenic disturbances such as cropland conversion, excessive livestock grazing, housing development, and fence collisions (Hagen et al. 2004, Wolfe et al. 2007). The greater prairie chicken (*T. cupido*) has also experienced large declines in portions of its range due to the combination of annual spring burning to create homogenous swards of grasses amenable for intensive, early season livestock grazing practices that have resulted in the loss and structural alteration of tallgrass prairie that is required for nesting (Ryan et al. 1998, Svedarsky et al. 2000, Robbins et al. 2002, Fuhlendorf and Engle 2004, Reinking 2005).

The purpose of our study was to evaluate patterns of sage-grouse lek persistence in the Bighorn Basin of Wyoming based on the individual and combined effects of many factors. Our specific objectives were to: 1) examine lek persistence based on landscape characteristics that may explain differences between occupied and unoccupied sage-grouse leks in the Bighorn Basin from 1980 to 2009, and 2) identify the relative and combined effects of landscape characteristics that were influential to lek persistence in the Bighorn Basin across the 30 years of the analysis. Identifying this suite of influential characteristics and their relationship to one another is a critical need that will provide a better understanding of landscape-scale issues inherent in conserving sage-grouse populations.

STUDY AREA

The Bighorn Basin includes Big Horn, Hot Springs, Park, and Washakie counties and encompasses 32,002 km^2 of north-central Wyoming. The Bighorn Basin is bordered by the Absoraka Mountains to the west, Beartooth and Pryor Mountains to the north, Bighorn Mountains to the east, and Bridger and Owl Creek Mountains to the south. The Bighorn Basin has an average valley elevation of 1,524 m (1,116 m minimum) composed of badland topography and intermittent buttes (USGS 2008*a*). Soil groupings include (1) aridic, coarse textured, (2) aridic, fine textured, (3) udic, cryic and (4) ustic, frigid soils (L. Munn, University of Wyoming, personal communication, 2008). The Bighorn Basin is semi-arid with average annual precipitation ranging from 12.7 to 38.1 cm.

The native flora of the Bighorn Basin includes perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*), Indian rice grass (*Achnatherum hymenoides*), needle and thread (*Hesperostipa comata*), and western wheatgrass

(*Pascopyrum smithii*); shrubs such as Wyoming (*Artemisia tridentata* ssp.*wyomingensis*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus viscidiflorus* and *Ericameria nauseosa*), and spineless horsebrush (*Tetradymia canescens*); and forbs/subshrubs including buckwheat (*Eriogonum* spp.), desert parsley (*Lomatium* spp.), milkvetch (*Astragalus* spp.), globemallow (*Sphaeralcea* spp.), prairie sagewort (*A. frigida*), pussytoes (*Antennaria* spp.), sego lily (*Calochortus nuttallii*) and Western yarrow (*Achillea millefolium*). Invasive species in the Bighorn Basin include cheatgrass (*Bromus tectorum*), Japanese brome (*B. japonicus*), Canada thistle (*Cirsum arvense*), hoary cress (*Cardaria draba*), knapweed (*Centaurea* spp.), and toadflax (*Linaria* spp.). Areas southeast of Worland, Wyoming are dominated by cheatgrass following a wildfire which burned approximately 40 km^2 of sagebrush in 1996. Fire rotations in Wyoming big sagebrush range in frequency from 200 to 350 years and are dependent on climate, topography, plant composition, and ecological site characteristics (Baker *In Press*).

Irrigated agricultural lands typically occurred at lower elevations than sagebrush rangelands and produced approximately 30% of Wyoming's agricultural output from crops such as alfalfa, barley, dry beans, field corn, oats, spring wheat, and sugar beets (Young et al. 1999). In 2008, the Bighorn Basin contributed over 80% of Wyoming's barley and sugar beet crops (Wyoming Agricultural Statistics Service 2009).

Dominant land uses in the sagebrush areas between agricultural and forested lands in the Bighorn Basin include livestock grazing; bentonite mining, with most current extraction occurring in lower elevation saltbush desert; and oil and gas extraction. Bentonite deposits in Wyoming make up 70% of the world's supply and mines in the Bighorn Basin produced over 50% of Wyoming's total bentonite production in 2008 (Wyoming Mining Association 2009).

Exploration of oil in the Bighorn Basin began in the early 1900s. Presently there are approximately 3,700 producing oil and gas wells (Wyoming Oil and Gas Conservation Commission 2009). Oil and gas fields in the Bighorn Basin produce about 28% of Wyoming's annual oil production and 1% of annual natural gas production (Big Horn Basin Local Work Group 2007). The Big Horn Basin Planning Area estimates a maximum potential of 1,865 new oil and gas wells from 2008–2027 (BLM 2009*a*).

In an effort to enhance wetlands, land health, and conditions for livestock, sage-grouse and other wildlife, the Cody and Worland BLM field offices conducted 156 prescribed burns (100 km^2 burned) and 55 mowing treatments (36 km^2 mowed) in sagebrush communities from 1980 to 2009. In addition, 91 wildfires burned 520 km^2 of sagebrush since 1980 (B. Wilson, BLM Cody Field Office, personal communication, 2009). There are 256 known greater sage-grouse leks in the Bighorn Basin (Wyoming Game and Fish Department, unpublished data, 2009). Of these leks, 60 (21%) have become unoccupied since 1980. This decline in persistent leks provided an opportunity to evaluate the influence of multiple factors that may potentially have influenced lek persistence in this region. Because about 70% of the leks in the Bighorn Basin occur on USDI Bureau of Land Management (BLM) land, we can further evaluate lek persistence in a landscape comprised of a relatively small amount of area in private ownership. By comparison, the proportion of public land in the Bighorn Basin is very similar to the proportion of public land (~70%) providing the remaining habitat to sage-grouse across their range (Knick et al. 2003). Through evaluating sagebrush community disturbances at a landscape scale, we can assess how these variables may impact lek persistence.

METHODS

Data Acquisition

We compiled multiple landscape feature classes using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California, USA). We categorized variables as follows: (1) sagebrush, (2) anthropogenic characteristics, (3) habitat treatments, and (4) wildfire (Table 3.2).

Sagebrush.—We obtained a sagebrush cover map from the Wyoming Geographic Information Science Center (2009) and extracted raster vegetation attributes that included Wyoming big sagebrush and mountain big sagebrush. We converted sagebrush raster canopy cover data into polygons to insure compatibility with other variables used in the analyses.

Anthropogenic characteristics.—We identified irrigated agricultural fields from data provided by the Wyoming Geographic Information Science Center (2009). Irrigated lands were used for our analysis because they are the primary form of crop agriculture in the Bighorn Basin. We obtained fence and road coverages from the Cody and Worland BLM Field Offices (B. Wilson, BLM Cody Field Office, personal communication, 2008). We placed a 50-m buffer on roads to represent the typical width and area disturbed by roads in semi-arid landscapes (Gelbard and Belnap 2003). Only paved and graded roads were used in our analysis due to the likelihood of inadequate records of unimproved roads in the Bighorn Basin (B. Wilson, BLM Cody Field Office, personal communication 2009). We acquired the pad locations for producing oil and gas wells from the Wyoming Oil and Gas Conservation Commission (2009).

Habitat treatments and wildfire.—We obtained polygons that mapped the locations of sagebrush mowing and prescribed burns and wildfires from 1980–2009 in the Bighorn Basin from the Cody and Worland BLM Field Offices (J. Mononi and T. Stephens, Cody BLM and Worland BLM, personal communication, 2008).

Lek Analysis Regions

Braun et al. (1977) recommended using a 3.0-km radius around leks to define sage-grouse breeding and nesting areas across their range of distribution and Connelly et al. (2000) further recommended energy related facilities be placed >3.2-km from active leks. The Bureau of Land Management uses a 3.2-km radius around leks to restrict the timing of oil and gas well drilling and construction activities during the sage-grouse breeding season (Bureau of Land Management 2009*c*). However, Wakkinen et al. (1992) cautioned that the common use of a 3.2-km radius area around leks may be insufficient for protecting nesting habitats because leks in areas with lower lek densities may not be proximal to one another and therefore may not include a large proportion of nesting sites. Research in Wyoming has shown the majority (64%) of sage-grouse nesting may occur within 5.0-km of leks in contiguous habitats (Holloran and Anderson 2005). Walker et al. (2007) indicated that sage-grouse population persistence requires maintaining sagebrush stands over larger areas (≥6.4 km) around leks. Wyoming Game and Fish Department (2010) recommends a 0.8-km circle placed around leks to reduce effects from powerline placement and a 1.0-km no surface occupancy radius to avoid disturbance to sage-grouse leks in energy development fields. We used multiple circular analysis regions to identify scales that were most important to sage-grouse lek persistence in the Bighorn Basin. Following the previously mentioned radii used to base management and conservation strategies, we used radii of 0.8 km, 1.0 km, 1.6 km, 3.2 km, 5.0 km, and 6.4 km placed around occupied and unoccupied leks for these analyses. We used a 1.6-km radius to evaluate whether the Wyoming Game and Fish Department's (2010) recommended 1.0-km radius to reduce effects of energy development to sage-grouse leks should be increased due to impacts on leks. We converted area for roads, agriculture, habitat treatments, wildfire, and sagebrush predictor variables into percentages (variable area divided by the area of each lek radius) for our analysis. We determined density of wells, length of fences, major powerlines, major pipelines, and roads within each lek radius.

To maintain accuracy and transparency in summarizing lek data, the analysis relied on terminology used by the Wyoming Game and Fish Department (WGFD) to monitor trends in sage-grouse lek counts. By basing lek assignment criteria on WGFD definitions (Table 3.1), we removed lek observations (*i*) for those leks in which for ≥1 decade, counts were not recorded, and (*ii*) for leks in which there was only one year of data. A lek was assumed occupied in those cases when it was observed at least once in a decade and was deemed active and observations during the following decade also supported its active status.

Data Analyses

We computed descriptive statistics, including two-sample *t*-tests to compare predictor variables between occupied and unoccupied sites. We used $\alpha = 0.10$ to determine statistical differences in these univariate comparisons. Prior to modeling, we assessed correlations between predictor variables to ensure multicollinearity did not exist in the set of predictor variables considered in the regression analyses. We removed one variable from each correlated pair when $|r| \geq 0.70$ (PROC CORR; SAS Institute 2004). We used binary logistic regression models to provide a fit to habitat predictor variables where the dependent data were 0 for unoccupied leks and 1 for occupied leks (Boyce and McDonald 1999, PROC LOGISTIC; SAS Institute 2003), where the logistic regression probability equation is: $\hat{p} = \dfrac{1}{1 + e^{(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \ldots + \beta_k X_k)}}$.

Through logistic regression we examined 45 models based on 8 alternative explanations of sage-grouse lek persistence patterns in our study area 1) roads and oil and gas wells, 2) wildfire, 3) wildfire and oil and gas wells, 4) agriculture and wildfire, 5) prescribed burning and wildfire, 6) agriculture and oil and gas wells, 7) infrastructure (i.e., bentonite mining, oil and gas wells, pipelines, and power lines), and 8) fencing and roads. The null model contained no predictor variables and was used to determine if logistic models provided a better fit for predicting lek persistence than a model containing no predictor variables. We evaluated model fit in simpler models (≤ 3 predictor variables) to avoid over fitting models (Burnham and Anderson 2002). We assessed the plausibility of each logistic regression model with Akaike's Information Criterion for small samples (AIC_c; Hurvich and Tsai 1989). Prior to regression analyses, we identified the scale with the best evidence for predicting lek persistence for each predictor variable by selecting the scale with the lowest AIC_c value. We then allowed the best scale for each predictor variable to compete with all other variables to create the final set of candidate models for predicting lek persistence. We selected the model with the lowest AIC_c value as the best-fitting model, and used the difference between AIC_c for the best model and AIC_c for the *i*th candidate model (Δ_i) to identify models competing with the best model. We followed the convention that models with $\Delta_i \leq 2$ were competitive with the best model, and models with $\Delta_i > 10$ were poorly supported (Burnham and Anderson 2002). Akaike weights (w_i) allowed us to assess the weight of evidence in favor of each model (Burnham and Anderson 2002). We ranked the relative importance of variables by summing w_i across all of the models in which they occurred (Burnham and Anderson 2002). To assess the influence of important variables on lek persistence, we created predictive probability of persistence curves for each variable from the top candidate model across the range of data for that parameter while holding other parameters in the model at their mean value (Aldridge and Boyce 2008). Current Wyoming Game and Fish Department recommendations state that non-core sage-grouse areas should maintain habitat conditions that will sustain at least a 50% probability of lek persistence (WYGFD 2010). As most of the Bighorn Basin encompasses core areas, we examined thresholds above 50% probability for each variable in the model-averaged estimates.

We used a variance decomposition technique to decompose relationships among the best fitting model (Battin and Lawler 2006). Through decomposition, variation from a single variable can be split into different components: (1) components that are purely explained by the individual response variable, and (2) components that are explained mutually by groups of response variables (shared components; Whittaker 1984). We ranked the influence of each predictor variable in the best-fitting model when the pure components of variation were greater than the shared components (Battin and Lawler 2006).

We used a five-fold cross validation procedure to evaluate the goodness-of-fit of the top predictive model (Boyce et al. 2002). To examine the discriminating ability of the best logistic regression model we evaluated the area under the receiver operating curve (ROC), which provided a measure of the best model's ability to discriminate between habitat characteristics at occupied leks (Hosmer and Lemeshow 2000). A perfect discrimination is represented by an ROC of 1.0 and a value of 0.5 or less represents no discrimination (Mason 1982). We used model averaging to address model uncertainty when competitive models were within 2 units of the best AIC_c model (Burnham and Anderson 2002). Following model averaging, calculations for cross-validation, receiver operating curve, odds ratios, and variance decomposition were used with model-averaged estimates.

RESULTS

We identified 183 leks (144 occupied leks and 39 unoccupied leks) for the analysis, with most leks becoming unoccupied from 1989 through 2004 (Fig. 3.1). We removed distance to nearest anthropogenic disturbance, sagebrush mowing percentage, and fence length from consideration in the modeling process due to high correlation with other variables and low predictive ability (i.e., AIC_c values were less than the AIC_c value for the null model). The variables, bentonite mining, major powerlines, and major pipelines had little or no influence in model selection and were removed from further modeling. We found higher well density and wildfire at unoccupied compared to occupied leks at 3 different radii around leks: 0.8 km, 1.0 km and 1.6 km (P <0.10;Table 3.3). All other predictor variables were not different between occupied and unoccupied leks at any scale. However, roads, well density, and prescribed burning approached significance (P = 0.107, P = 0.138, and P = 0.142 respectively) at the 6.4 km-radius scale around leks (Table 3.3). We evaluated a total of 45 models and focused on the most predictive models that had AIC_c values lower than the null model. Among the top 13 candidate models, 3 models were highly competitive ($\Delta AIC_c < 2$): density of oil and gas wells in a 1.0-km radius; percent area of wildfire in a 1.0-km radius; and roads in a 6.4-km radius around sage-grouse leks (Table 3.4). Logistic regression probability equations for the top three models were as follows:

$$\hat{p} = \frac{1}{1 + e^{(1.499 - 0.413\, X_{Wells} - 0.016\, X_{Wildfire})}} \tag{1}$$

$$\hat{p} = \frac{1}{1 + e^{(1.397 - 0.394\, X_{Wells})}} \tag{2}$$

$$\hat{p} = \frac{1}{1 + e^{(2.282 - 0.355\, X_{Wells} - 0.017 X_{Wildfire} - 0.082 X_{Roads})}} \tag{3}$$

Unoccupied leks had 1.1-times greater percentage of road area in a 6.4-km radius; 3.1-times greater percentage of wildfires in a 1.0-km radius; and 10.3-times greater density of wells in a 1.0-km radius than occupied leks (Table 3.3). The receiver operating curve for the best model (0.58) indicated this model was fair at discriminating between occupied and unoccupied lek habitats based on the presence of wildfire and oil and gas wells in a 1.0-km radius and roads in a 6.4-km radius around sage-grouse leks (Hosmer and Lemeshow 2000). The cross-validation analysis indicated the best model performed moderately to predict lek persistence (r_s = 0.37, P = 0.293, n = 10). Relative importance weights for the most important predictor variables were oil and gas well density/1.0-km radius around leks (0.84), percentage wildfire/1.0-km radius around leks (0.57), and percentage of road area/6.4-km radius around leks (0.42). The relative importance for other variables evaluated across models was ≤ 0.08.

The model-averaged parameter estimate for oil and gas well density at the 1.0-km radius was –0.348 (SE = 0.209; 95% CI: –0.695,–0.001); percent wildfire at the 1.0-km radius was –0.011 (SE = 0.007; 95% CI: –0.022, –0.001); and percent road area at the 6.4-km radius was –0.061 (SE = 0.049; 95% CI:–0.143, 0.019). Model-averaged parameter estimates yielded the logistic regression probability equation:

$$\hat{p} = \frac{1}{1 + e^{\left(1.533 - 0.348\, X_{Wells} - 0.011 X_{Wildfire} - 0.061 X_{Roads}\right)}}.$$

The odds of lek persistence with every 1 unit increase in oil and gas wells within a 1.0-km radius of leks was 0.71 (95% CI: 0.50–0.99), indicating that the odds of lek persistence decreased by 29% with each additional well in a 1.0-km radius around a lek. Odds of lek persistence with every 1% increase in the area of roads in a 6.4-km radius around a lek was 0.94 (95% CI: 0.87–1.02), suggesting the odds of lek persistence decreased by 6% with every 1% increase in roads in a 6.4-km radius around leks. Odds of lek persistence with every 1% increase in wildfire in a 1.0-km radius was 0.99 (95% CI: 0.98–0.99), suggesting the odds of lek persistence decreased by 1% with every 1% increase in the area burned by wildfire in a 1.0-km radius around leks. Because the 95% CI around the model-averaged odds ratios of wells and wildfire did not overlap 1.0, we suggest that both variables were most influential in the model-averaged estimates. The probability of persistence of sage-grouse leks in the Bighorn Basin was negatively affected when oil and gas well densities in a 1.0-km radius were >2 wells/km^2 (Fig. 3.2) and percent area of roads in a 6.4-km radius around leks was >20% (Fig. 3.3). Oil and gas well density in a 1.0-km radius around leks explained 46% of the pure variation in the lek persistence model; wildfire explained 35% of pure variation; and roads explained 15% of the pure variation in the model. Only 3.6% of total variation was explained by shared components.

DISCUSSION

Our approach of examining a suite of potential stressors at multiple scales to explain differences between occupied and unoccupied sage-grouse leks met the objective of identifying effects of influential disturbances to sage-grouse lek persistence. We note that habitat enhancement treatments (mowing and prescribed burning) and bentonite mining were not influential predictors of lek persistence at the landscape scales evaluated. However, we found distinguishable differences among lek persistence in the Bighorn Basin, with a higher percentage of roads, wildfire, and density of wells surrounding unoccupied compared to occupied leks. Model-averaged estimates predicted that increases in oil and gas well density and percent area of wildfire in a 1.0-km radius around leks, and percent area of roads in a 6.4-km radius around leks were detrimental to lek persistence in the Bighorn Basin from 1980 to 2009.

Although odds ratios suggest the area of roads within a 6.4-km radius of leks was not important in our modeling, we believe roads were still influential in lek persistence in the Bighorn Basin. The relative importance of roads was much greater than other variables in the analysis and roads explained 15% of the pure variation in the model-averaged estimates, suggesting roads were actually influential in logistic models. Other studies have shown negative impacts resulting from roads such as fragmentation (Braun 1998, Knick et al. 2003), invasion of exotic plants (Gelbard and Belnap 2003), avoidance of males on leks (Holloran 2005), lek abandonment (Braun 1986), lowered nest initiation rates (Lyon and Anderson 2003), and avoidance of nesting females (Aldridge and Boyce 2007). Gunnison sage-grouse occupancy probabilities were positively correlated with increasing distance to roads (Olyer-McCance 1999). Lek attendance by males declined when leks were within 3-km of a main haul road compared to control leks (i.e., leks situated more than 6.1-km from a main haul road) and road activity negatively affected the number of displaying males on leks in portions of Wyoming (Holloran 2005). Along Interstate 80 in Wyoming, there are now no occupied leks within 2 km of the interstate (Connelly et al. 2004). The reason roads did not have a significant odds ratio may be due to the Bighorn Basin having a lower density of oil and gas wells compared to other portions of the state that are more heavily traveled. Because the variable roads had high relative importance in model selection, roads may have indirect effects on lek persistence that our analysis was unable to detect. The main source of disturbance following the drilling of a well is mostly caused by road traffic (Lyon and Anderson 2003). We did not examine intensity or human use of roads, but Remington and Braun (1991) found declines in the number of displaying males when haul roads for surface coal mining activities were close to leks. There may be a threshold where the influence of roads on lek persistence may increase as development activity increases. Furthermore, spatial data sets for road coverages are known to underrepresent secondary or paved roads (Aldridge et al. 2008) which could cause our inability to detect a significant effect on lek persistence.

Results indicate density of wells around leks was the most important predictor of lek persistence, but alone, it did not explain as much of the influence on lek persistence as when it was combined with the area of roads and wildfire around leks. Because these factors are related, our results show support for the synergistic influences of these 3 disturbance factors on sage-grouse lek persistence over the 30 years of the analysis. These results are of particular importance because they corroborate findings on sage-grouse lek persistence from others studies conducted in areas with much higher levels of disturbance (Connelly et al. 2000*b*, Holloran 2005, Walker et al. 2007, Harju et al. 2010). We provided arguable evidence (magnitude of effect in estimated means, variable importance values, odds ratios and confidence intervals, variance decomposition) that wells and wildfire were most influential to lek persistence.

Because no single factor has led to the decline in sage-grouse populations across their range, researchers need to examine the unintended additional stressors that result from anthropogenic activity (Johnson et al. 2010). Recent studies have documented the indirect effects of oil and gas development on sage-grouse; however, the mechanisms that indirectly lead to the response of sage-grouse populations to this development have rarely been reported (but, see Holloran et al. 2010). Disturbances from oil and gas development include disrupting breeding (Lyon and Anderson 2003), declines in lek persistence and male lek attendance (Holloran 2005, Walker et al. 2007, Doherty et al. 2010, Harju et al. 2010), lower yearling male recruitment to impacted leks (Kaiser 2006, Holloran et al. 2010), lower yearling male and yearling female survival (Holloran et al. 2010), higher chick mortality (Aldridge and Boyce

2007), avoidance of wintering habitats (Doherty et al. 2008), decreased nest initiation rates (Lyon and Anderson 2003), increased distances of nesting sites from leks (Lyon and Anderson 2003), and lower annual female adult survival (Holloran 2005). Fragmentation, due to energy development, can lead to increasing numbers of predators that prey on nests, young, and adult sage-grouse (Steenhof et al. 1993, Connelly et al 2000*b*, Vander Haegen et al. 2002, Coates and Delehanty 2010). Lek persistence in the Powder River Basin of northeastern Wyoming was found to decrease 2–5 times inside development areas with >12 wells per 32.3 km^2 compared to undeveloped landscapes (Doherty et al. 2010). The Bighorn Basin has lower reserves of oil and gas than many other regions of Wyoming (USGS 2008*b*). By comparison, there is an estimated 72 million barrels of undiscovered oil, and 13 million barrels of undiscovered natural gas in the Bighorn Basin compared to 649 million barrels of undiscovered oil and 131 million barrels of undiscovered natural gas in the Powder River Basin (USGS 2008*b*). However, our study supports findings of other studies in areas with greater levels of energy development that demonstrate energy development negatively affects lek persistence (Holloran et al. 2010, Walker et al. 2007, Harju et al. 2010).

When evaluating the influence of energy development on leks in Wyoming, Doherty et al. (2010) detected a 55% decline in males attending leks when well densities were 13–39 wells within a 3.2-km radius in Sage-Grouse Management Zone II (Stiver et al. 2006), which includes the Bighorn Basin. Harju et al. (2010) reported 91% fewer males attending leks when ≥ 1 well was within a 0.4-km radius in the Bighorn Basin compared to leks with no wells within 0.4-km radius. The reason we found oil and gas development within the 0.8 to 1.6-km scale around leks to negatively affect lek persistence is because this analysis encompassed 183 leks, while Harju et al. (2010) focused on 65 leks from the Bighorn Basin, which were located in areas with greater levels of energy development than the larger and more geographically distributed sample we evaluated. Walker et al. (2007) found negative effects of CBNG within 0.8-km and 3.2-km of leks in the Powder River Basin of northeastern Wyoming and recommended reevaluating stipulations that prohibited development within 0.4-km of leks and stated this stipulation was inadequate to promote lek persistence. Our results show that occupied and unoccupied leks differed significantly in well density at distances up to 1.6-km radius from leks.

Because the Bighorn Basin has not experienced rapid landscape changes resulting from development of natural-gas fields resembling the intensive development levels found in other portions of Wyoming, the 1.0-km scale of well density we found to be most influential on sage-grouse lek persistence, when combined with other variables, was likely related to the low intensity and relatively isolated nature of development in the Bighorn Basin. The Bighorn Basin has ~3,700 producing oil and gas wells compared to the Powder River Basin, which has >35,000 producing wells with 68,000 wells authorized on public lands (Naugle et al. *In Press*) and the Green River Basin, which had >7,800 active and potential wells in 2003 (Holloran 2005). Because of the higher number of wells, the impacts of development may be much more intense in the Powder River and Green River Basins and gives further support for the different scales (1.0-km and 6.4-km) we found in combination to most influence lek persistence in the Bighorn Basin. Even though our study area has lower energy development pressure compared to other areas in Wyoming, the analysis nevertheless agrees with recent studies that suggest the need to reevaluate current stipulations and management practices in areas with energy development and to incorporate regional research in management decisions based on local sage-grouse populations (Walker et al. 2007, Doherty et al. 2010, Harju et al. 2010, Holloran et al. 2010).

Baker (*In Press*) estimated recovery of mountain big sagebrush to pre-burn status for two recovery tracks; the fast track may have full recovery by 25–35 years following fire and the slow track may take 75 years or more for full recovery following fire. Recovery of Wyoming big sagebrush following fire is much often slower than mountain big sagebrush and is highly variable (Baker *In Press*). Reduction in suitable sage-grouse nesting and brood-rearing habitat in southeastern Idaho occurred when approximately 30% of the study area was burned (Nelle et al. 2000). Wildfire can have indirect effects on grouse by reducing insect populations (Fischer et al. 1996) needed by chicks for growth and development (Johnson and Boyce 1990). Fragmented shrubsteppe increases sage-grouse nest failures and implies risk of predation in areas with higher levels of grass-forb dominated habitat along edge habitats disturbed by fire (Shepherd 2005). Developing roads can accelerate the dispersal and establishment of invasive plant species (Gelbard and Belnap 2003, Bergquist et al. 2007), and consequently shorten fire return intervals (Levine et al. 2003) causing further sage-grouse habitat loss.

Loss of sagebrush, through wildfires and other means, redirects the composition of sagebrush communities to dominance by undesirable plants (Prevéy et al. 2010). The propagation of cheatgrass increases the likelihood of future fires that can lead to the loss of perennial grasses and shrubs (Crawford et al. 2004). Cheatgrass has been estimated to cover >80 km^2 of the Bighorn Basin (Wyoming Pest Detection Program 2009). Fire is even a larger threat in degraded sagebrush habitats because residual shrub patches may ultimately become dominated by invasive plants that promote higher fire return intervals and further negate efforts of restoring habitats to previous sagebrush stages due to inaccessible seed banks and inadequate recovery periods (Knick and Rotenberry 1997, Connelly et al. 2000*a, b*; Menakis et al. 2003, Jessop and Anderson 2007, Prevéy et al. 2010).

Our persistence modeling suggests a suite of interrelated variables that can negatively affect the persistence of sage-grouse leks in the Bighorn Basin. Theoretically, as well numbers increase, the likelihood of additional road development increases due to drilling activities and accessibility needs to monitor and maintain these wells. This increase in the amount of roads around wells can lead to higher dispersal of invasive plants that often promote higher frequencies of wildfire.

Across their range, sage-grouse populations have been declining due to numerous, and sometimes immeasurable, cumulative effects causing fragmentation, loss and degradation of suitable habitat (Knick et al. 2003). Because we found higher levels of wells, wildfire, and roads in the unoccupied lek radii (Table 3.3), we suggest there is some relationship among these variables and, and that individually, each factor has contributed to lek abandonment in sage-grouse populations in the Bighorn Basin. Our findings coincide with other research indicating human disturbance is a leading factor in sage-grouse population decline and persistence (Swenson et al. 1987, Lyon and Anderson 2003, Connelly et al. 2004, Holloran and Anderson 2005, Smith et al. 2005, Aldridge and Boyce 2007, Walker et al. 2007), but also suggests synergistic effects of interrelated factors on lek persistence.

MANAGEMENT IMPLICATIONS

Because they are interrelated, increasing roads, energy development, and wildfire are predicted to result in loss of more sage-grouse leks in the Bighorn Basin. Consequently, conservation efforts should be focused on mitigating disturbances associated with energy development, roads, and wildfire to stem the decline of sage-grouse leks. Wildfire suppression and minimizing well construction strategies are needed in areas with larger numbers of sage-grouse leks. The BLM

(2009*b*) in Nevada has prioritized wildfire suppression around leks and has developed precautionary measures to reduce risks associated with wildfire to sage-grouse including localized habitat maps, suppression tactics, training programs, avoiding leks when creating wildfire suppression facilities, and proper cleaning of field vehicles to prevent noxious weed spread into sage-grouse habitat. Braun et al. (2005) also recommended the need for vigorous wildfire suppression to protect and maintain existing sage-grouse habitats. Our results suggest focusing wildfire prevention tactics not just within a minimum 1.0-km radius around leks. Rather, we found evidence for managers to extend suppression tactics to a 1.6-km radius around leks because unoccupied leks had 2.8-times the percentage of wildfire area compared to occupied leks. Scales at 3.2-, 5.0-, and 6.4-km radii showed no discernable difference in area of wildfire between occupied and unoccupied leks.

Current Bureau of Land Management (BLM 2009*c*) and Wyoming Game and Fish Department (2010) recommendations restrict surface occupancy within a 1.0-km region around leks within sage-grouse core areas and a 0.4-km region around leks in sage-grouse non-core areas and inhibiting development activities between 1800 and 0800 hours during the sage-grouse breeding season (15 March–15 May; Wyoming Game and Fish Department 2010). Because the Bighorn Basin occupies core and non-core sage-grouse habitats, we recommend placing at least a 1.6-km no surface occupancy region around each lek in core and non-core sage-grouse habitats to promote probability of lek persistence in the Bighorn Basin. We found no effect at scales 3.2-km or greater around leks. Furthermore, timing restrictions of disruptive activity within a 3.2-km radius around leks is commonly implemented during breeding seasons (15 March–15 May), but nesting, brood-rearing, and wintering habitats are also important to sage-grouse population persistence. Because wildfire and human development can impact sagebrush communities for long periods of time, not just seasonally, we agree with Walker et al. (2007) who suggested more effective management practices than timing restrictions due to impacts that dramatically influence lek persistence during other periods of the year.

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Table 3.1. Terminology used by Wyoming Game and Fish Department (unpublished data, 2006) to monitor greater sage-grouse leks.

Term	Definition
Active lek	Lek that has attending male sage-grouse during the strutting season
Inactive lek	Lek where there is no attending male sage-grouse during the entire strutting season. Absence of sign (droppings/feathers) as well as visual absence of activity are needed for this designation. Aerial surveys are not sufficient for this status designation
Occupied lek	Lek that has been active during at least one strutting season within the prior ten years
Unoccupied lek	Lek that has been abandoned or destroyed
Abandoned lek	Lek in suitable habitat that has not been active in a 10 year period. Must be inactive for at least 4 non consecutive strutting seasons during the 10 year period. Abandoned leks are surveyed at least once every 10 years since its designation to ascertain whether the lek has become reoccupied by sage-grouse
Destroyed lek	Formerly active lek that has become destroyed or unsuitable for sage-grouse strutting activities. This includes sites that have been paved, converted to agricultural land, strip-mined, or have long-term habitat alteration. These leks are no longer surveyed unless the area has been reclaimed to suitable sage-grouse habitat

Table 3.2. Predictor variables used for greater sage-grouse lek persistence models in the Bighorn Basin, Wyoming, USA, 1980–2009. Percentage data were computed as the proportion of area (× 100) of each respective variable within circular analysis regions with radii of 0.8, 1.0, 1.6, 3.2, 5.0, and 6.4 km.

Category	Variable	Description
Anthropogenic	Agriculture (%)	Percentage of land irrigated at corresponding lek radii
	Agriculture distance (m)	Distance to closest irrigated agriculture field
	Anthrop distance (m)	Distance to nearest anthropogenic disturbance (road, well, fence, bentonite mine, exurban development, pipeline, or agriculture)
	Fence length (m)	Length of fence at corresponding lek radii
	Fence distance (m)	Distance to nearest fence
	Roads (%)	Percentage of the 50 m buffered roads at corresponding lek radii
	Roads distance (m)	Distance to nearest road
	Wells (no.)	Number of producing wells in corresponding lek radii

Table 3.2. Continued

Category	Variable	Description
	Well distance (m)	Distance to closest oil and gas well
Sagebrush	Sagebrush (%)	Percentage of sagebrush at corresponding lek radii
Habitat treatments	Mow[a] (%)	Percentage of land treated by mechanical mowing at corresponding lek radii
	Mow distance[a] (m)	Distance to nearest mechanical mowing
	Prescribed burn (%)[b]	Percentage of land treated by prescribed burning at corresponding lek radii
	Prescribed burn[b] (m)	Distance to nearest prescribed burn
Wildfire	Wildfire[b]	Percentage of land treated by wildfire at corresponding lek radii
	Wildfire distance [b](m)	Distance to closest wildfire

[a] Mowing treatments occurred during 2000–2009.

[b] Prescribed burning and wildfire occurred during 1980–2009.

Table 3.3. Descriptive statistics for predictor variables potentially influencing greater sage-grouse lek persistence (n = 144 occupied and n = 39 unoccupied leks) in the Bighorn Basin, Wyoming, USA, 1980–2009. Distance refers to the distance (m) from lek to nearest variable (e.g., nearest irrigated agricultural field). Scale refers to the 6 different circular analysis regions around leks 0.8, 1.0, 1.6, 3.2, 5.0, 6.4 km radii around leks).

Category	Scale	Occupied		Unoccupied		*t*	*df*	*P*
		Mean	SE	Mean	SE			
Agriculture								
	Distance (m)	3,893.43	213.99	3,935.32	357.02	–0.10	68	0.920
	0.8 km	0.17	0.12	0.24	0.23	–0.27	61	0.788
	1.0 km	0.23	0.16	0.21	0.21	0.05	181	0.957
	1.6 km	0.27	0.17	0.26	0.25	0.04	77	0.970
	3.2 km	0.93	0.21	0.50	0.37	1.00	65	0.321
	5.0 km	1.74	0.29	1.05	0.37	1.18	181	0.241
	6.4 km	2.26	0.32	1.89	0.52	0.60	71	0.587
Fence length (m)								
	Distance (m)	1,022.93	83.80	952.80	147.62	0.41	65	0.681
	0.8 km	819.43	73.42	1,051.54	185.44	–1.36	181	0.176
	1.0 km	1,363.11	107.27	1,555.92	250.77	–0.79	53	0.483
	1.6 km	3,898.13	243.02	3,864.32	460.00	0.06	61	0.948
	3.2 km	16,697.20	762.58	16,595.22	1,346.75	0.07	65	0.948
	5.0 km	42,483.63	1,638.73	40,481.74	2,491.66	0.67	75	0.544
	6.4 km	69,031.41	2,399.73	64,334.30	3,819.37	1.04	71	0.301

Table 3.3 Continued

Category	Scale	Occupied		Unoccupied		*t*	*df*	*P*
		Mean	SE	Mean	SE			
Human disturbance								
	Distance (m)	50,774.35	13,466.38	270.83	43.48	1.95	181	0.053
	0.8 km	4.46	0.76	5.42	1.56	–0.55	58	0.585
	1.0 km	4.28	0.68	5.45	1.69	–0.74	181	0.460
	1.6 km	4.39	0.55	5.15	1.57	–0.46	181	0.567
	3.2 km	6.19	0.76	4.93	1.04	0.80	181	0.423
	5.0 km	7.36	0.79	5.30	0.74	1.32	181	0.188
	6.4 km	8.02	0.79	6.81	0.85	0.76	181	0.449
Mow								
	Distance (m)	10,581.14	685.46	8,989.98	1,270.80	1.10	62	0.275
	0.8 km	4.14	1.46	3.86	2.11	0.09	181	0.928
	1.0 km	3.92	1.40	3.66	2.05	0.11	77	0.916
	1.6 km	3.71	1.27	3.34	1.92	0.16	75	0.875
	3.2 km	2.42	0.80	3.17	1.63	–0.41	58	0.680
	5.0 km	1.76	0.50	2.34	1.06	–0.49	57	0.624
	6.4 km	1.44	0.38	1.84	0.76	–0.48	58	0.634
Prescribed burning								
	Distance (m)	8,571.04	653.59	8,690.27	1,644.85	–0.08	181	0.938
	0.8 km	3.02	1.07	0.73	0.51	1.10	181	0.275
	1.0 km	3.07	1.02	0.91	0.64	1.08	181	0.282
	1.6 km	2.67	0.79	1.45	0.76	0.77	181	0.440

Table 3.3 Continued

Category	Scale	Occupied		Unoccupied		*t*	*df*	*P*
		Mean	SE	Mean	SE			
	3.2 km	1.60	0.46	1.71	0.60	–0.11	181	0.909
	5.0 km	1.27	0.29	1.74	0.54	–0.77	62	0.442
	6.4 km	1.18	0.23	1.97	0.59	–1.48	181	0.142
Road								
	Distance (m)	280.50	28.42	348.49	42.95	–1.32	75	0.251
	0.8 km	11.83	0.56	10.97	1.11	0.69	59	0.491
	1.0 km	10.98	0.48	10.91	0.98	0.06	58	0.952
	1.6 km	10.02	0.39	10.59	0.82	–0.63	57	0.531
	3.2 km	9.27	0.33	9.92	0.66	–0.90	58	0.373
	5.0 km	9.16	0.29	9.77	0.49	–1.07	67	0.290
	6.4 km	9.14	0.27	10.04	0.48	–1.63	64	0.107
Road length (m)								
	0.8 km	2,329.86	95.65	2,065.98	197.57	1.20	57	0.234
	1.0 km	7,955.08	270.85	3,264.40	280.58	0.61	55	0.543
	1.6 km	3,453.74	129.80	7,926.32	546.94	0.05	58	0.963
	3.2 km	29,506.42	827.93	29,806.46	1,815.00	–0.15	55	0.881
	5.0 km	71,310.69	1658.19	71,677.27	3,377.77	–0.10	58	0.923
	6.4 km	116,524.54	2,411.88	119,987.13	5,412.49	–0.58	54	0.561
Sagebrush								
	0.8 km	7.34	0.78	7.49	1.70	–0.08	55	0.936
	1.0 km	7.16	0.74	7.65	1.68	–0.26	54	0.793

Table 3.3Continued

Category	Scale	Occupied		Unoccupied		*t*	*df*	*P*
		Mean	SE	Mean	SE			
	1.6 km	7.00	0.69	7.39	1.53	–0.23	54	0.817
	3.2 km	7.13	0.60	7.32	1.39	–0.13	53	0.900
	5.0 km	7.19	0.56	7.28	1.32	–0.06	53	0.954
	6.4 km	7.20	0.53	7.25	1.26	–0.04	53	0.967
Well density								
	Distance (m)	8,678.91	555.45	6,255.94	793.89	2.12	181	0.036
	0.8 km	0.04	0.02	0.44	0.25	–2.84	181	0.005
	1.0 km	0.07	0.03	0.72	0.42	–2.88	181	0.004
	1.6 km	0.25	0.08	1.77	1.12	–2.53	181	0.012
	3.2 km	3.83	1.45	6.18	3.71	–0.69	181	0.490
	5.0 km	10.10	3.18	14.08	5.64	–0.61	64	0.542
	6.4 km	16.97	3.93	30.51	8.09	–1.50	57	0.138
Wildfire								
	Distance (m)	8,019.11	474.94	7,236.53	1,045.10	0.68	55	0.498
	0.8 km	3.22	1.27	10.23	4.57	–2.06	181	0.041
	1.0 km	3.26	1.27	10.04	4.53	–2.00	181	0.047
	1.6 km	3.51	1.28	9.65	4.41	–1.82	181	0.070
	3.2 km	4.44	1.25	8.57	3.98	–1.30	181	0.194
	5.0 km	4.54	1.10	7.75	3.43	–1.16	181	0.247
	6.4 km	4.48	1.00	7.29	2.89	–1.15	181	0.251

Table 3.4. Fit statistics for the top 13 candidate models explaining sage-grouse lek persistence in the Bighorn Basin, Wyoming, USA, 1980-2009. Each logistic regression model was based on *n* = 144 occupied and *n* = 39 unoccupied leks. Models are listed according to the model best fitting the data and ranked by (Δ_i), the difference between the model with the lowest Akaike's Information Criterion for small samples (AICc) and the AICc for the current model. For each logistic regression model, the –2 × log likelihood (–2LL), number of estimated parameters (K), and Akaike weights (*wi*) for each model are also presented. Circular analysis region around leks (km) follow variable names (i.e., 1.0, 5.0, 6.4).

Model name	**-2LL**	**K**	**AICc**	**ΔAICc**	***wi***
Wildfire1.0 + WellDensity1.0	179.311	3	185.445	0.000	0.263
Wildfire1.0 + Road6.4 + WellDensity1.0	177.516	4	185.741	0.296	0.226
WellDensity1.0	183.059	2	187.126	1.681	0.113
WellDensity1.0 + Road6.4	181.803	3	187.937	2.492	0.076
Agriculture5.0 + WellDensity1.0	181.906	3	188.040	2.595	0.072
WellDensity1.0 + Prescribedburn6.4	182.205	3	188.339	2.894	0.062
Prescribedburn6.4 + Road6.4	184.770	3	188.837	3.392	0.048
Wildfire1.0 + Road6.4	183.085	3	189.219	3.774	0.040
Global	175.341	7	189.981	4.536	0.027
Wildfire1.0	186.317	2	190.384	4.939	0.022
Agriculture5.0 + Road6.4	184.725	3	190.859	5.414	0.018
Road6.4	187.130	2	191.197	5.752	0.015
Wildfire1.0 + Prescribedburn6.4	185.090	3	191.224	5.779	0.015

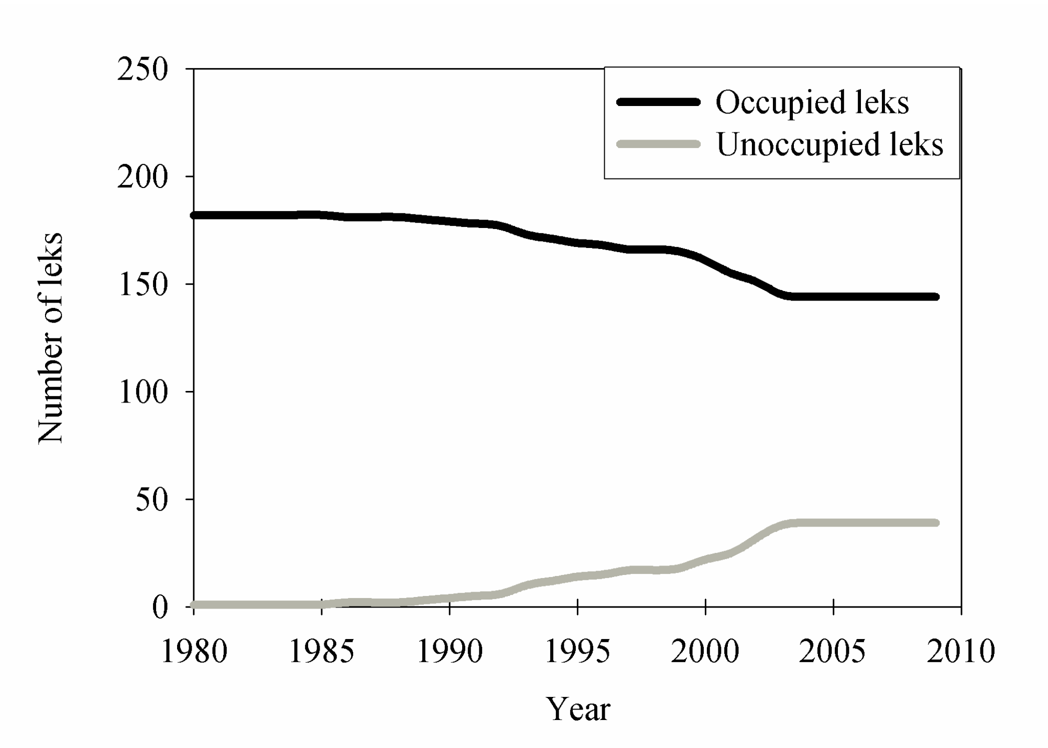

Figure 3.1. Change in occupied and unoccupied greater sage-grouse leks in the Bighorn Basin, Wyoming, USA, 1980–2009. There were a total of 256 leks in the Bighorn Basin during this time period, 183 of which had sufficient data for the analysis. Since 1980, 39 of these 183 leks became unoccupied, which is represented in this figure.

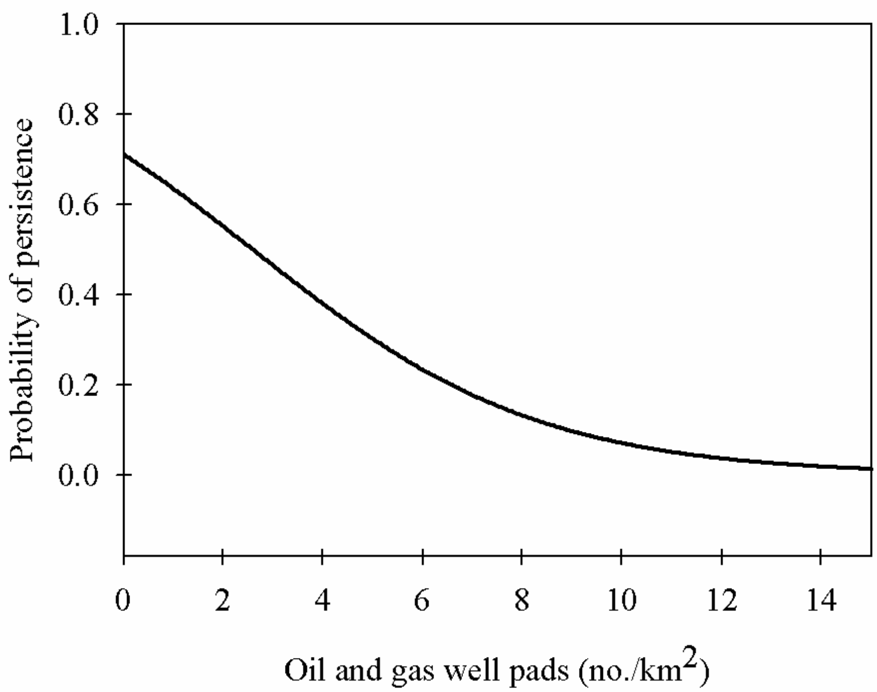

Figure 3.2. Probability of greater sage-grouse lek persistence as a function of model-averaged estimates of oil and gas wells (number/1.0 km^2) within a 1.0-km radius from a lek while holding other model parameters at their mean value in the Bighorn Basin, Wyoming, USA, 1980–2009. The area of wildfire was held constant at its mean value within a 1.0-km radius and the area of roads was held constant at its mean value within a 6.4-km radius around sage-grouse leks.

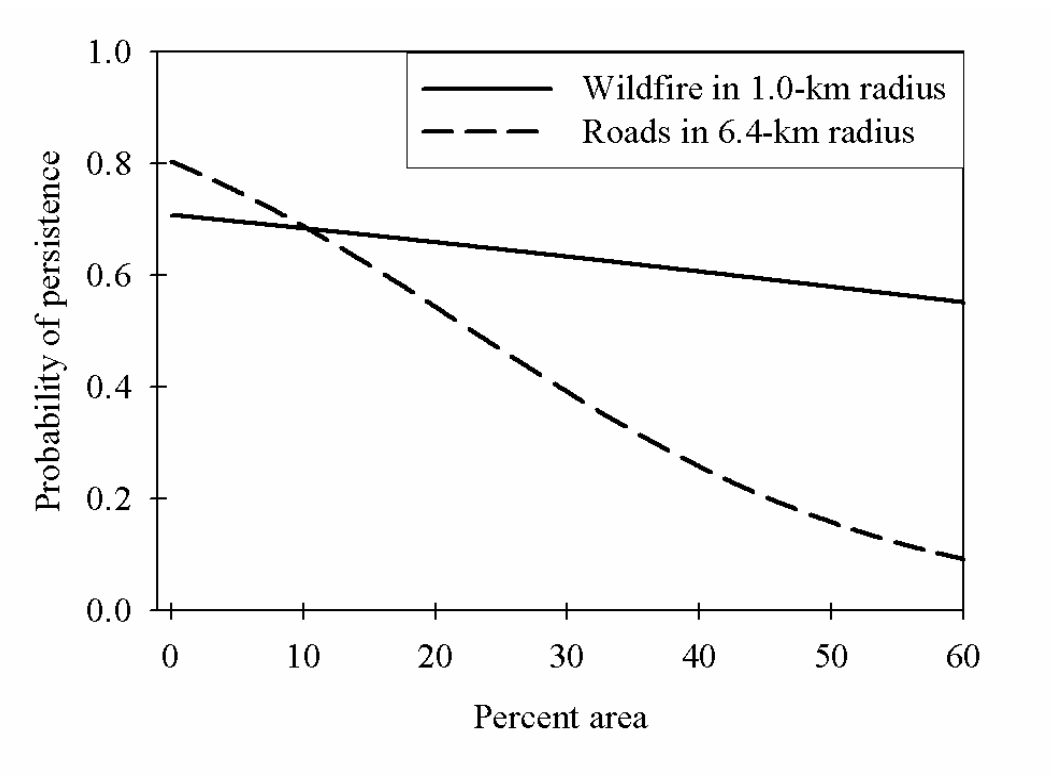

Figure 3.3. Probability of greater sage-grouse lek persistence as a function of model-averaged estimates of wildfire (% area in a 1.0-km radius around leks) and roads (% area in a 6.4-km radius around leks) while holding well density (no./1.0 km^2) constant at its mean value in the Bighorn Basin, Wyoming, USA, 1980–2009.