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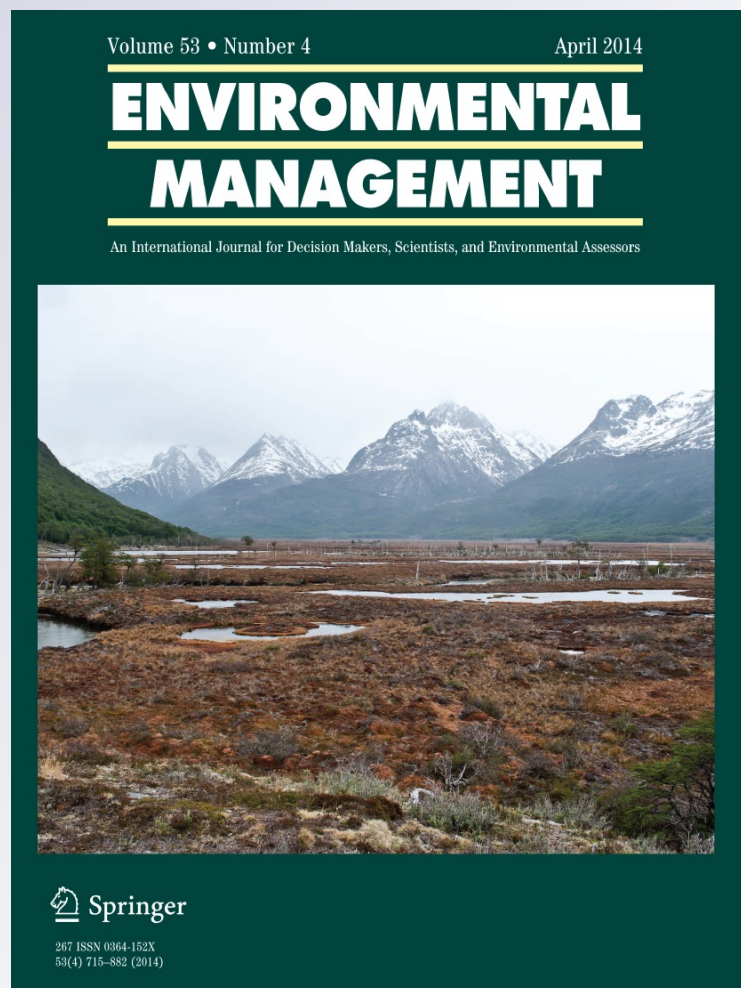
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Forb, Insect, and Soil Response to Burning and Mowing Wyoming Big Sagebrush in Greater Sage-Grouse Breeding Habitat

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Abstract Wyoming big sagebrush (*Artemisia tridentata wyomingensis* A. t. Nutt. ssp. *wyomingensis* Beetle and Young) communities provide structure and forbs and insects needed by greater sage-grouse (*Centrocercus urophasianus*) for growth and survival. We evaluated forb, insect, and soil responses at six mowed and 19 prescribed burned sites compared to 25, paired and untreated reference sites. Sites were classified by treatment type, soil type, season, and decade of treatment (sites burned during 1990–1999 and sites burned or mowed during 2000–2006). Our objective was to evaluate differences in ten habitat attributes known to influence sage-grouse nesting and brood rearing to compare responses among treatment scenarios. Contrary to desired outcomes, treating Wyoming big sagebrush through prescribed burning or mowing may not stimulate cover or increase nutrition in food forbs, or increase insect abundance or indicators of soil quality compared with reference sites. In some cases, prescribed burning showed positive results compared with mowing such as greater forb crude protein content (%), ant (Hymenoptera; no./trap), beetle (Coleoptera/no./trap), and grasshopper abundance (Orthoptera; no./sweep), and total (%) soil carbon and nitrogen, but of these attributes, only grasshopper abundance was enhanced at burned sites compared with reference sites in 2008. Mowing did not promote a statistically significant increase in sage-grouse

nesting or early brood-rearing habitat attributes such as cover or nutritional quality of food forbs, or counts of ants, beetles, or grasshoppers compared with reference sites.

Keywords *Centrocercus urophasianus* · Forbs · Greater sage-grouse · Insects · Mowing · Prescribed burning · Soil quality

Introduction

Big sagebrush (*Artemisia tridentata* Nutt.)-dominated rangeland is the largest potential vegetation type in the western United States (Miller et al. 2011), historically being the major shrub on 600,000 km² (Beetle 1960). However, landscape changes stemming from anthropogenic disturbances have reduced big sagebrush to an estimated 50–60 % of its historical distribution (Schroeder et al. 2004; Miller et al. 2011). Sagebrush communities provide habitat to a diversity of wildlife including 93 bird, 92 mammal, and 58 reptile, and amphibian species (Welch 2005). The quality of wildlife habitat in remaining sagebrush is an important conservation issue owing to degradation of these communities by invasive exotic herbaceous species and encroaching conifers (Davies et al. 2011).

A critical function of sagebrush habitats is to provide forbs and insects needed by chick and adult greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) for growth and survival. Specifically, the abundance and quality of food forbs, insect abundance, and the quality of soils that influence plant growth are measurable characteristics of the quality of sagebrush habitats used by sage-grouse during the breeding season (prelaying, lekking, nesting, and early brood-rearing). Forbs provide an important source of calcium, phosphorus, and protein for

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prelaying females and for the growth and development of juvenile sage-grouse (Johnson and Boyce 1990; Barnett and Crawford 1994; 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). Consequently, estimating the abundance of insects is fundamental to evaluating the quality of sage-grouse brood-rearing habitat. Insects that are important to juvenile and adult sage-grouse include ants (Hymenoptera), beetles (Coleoptera), and grasshoppers (Orthoptera; Patterson 1952; Johnson and Boyce 1990; Connelly et al. 2000). Healthy soil is the foundation of stable, productive terrestrial ecosystems. Soil, including plant roots, provides habitat for many terrestrial organisms, 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). Furthermore, rangeland forage production and wildlife habitat are dependent on the general productivity and quality of soils (National Research Council 1994; Karlen et al. 1997).

The application of sagebrush treatments has generated debate regarding whether the responses in sagebrush communities benefit sage-grouse nesting and early brood-rearing habitats (Winward 1991; Pyle and Crawford 1996; Crawford et al. 2004; Beck et al. 2009; Rhodes et al. 2010; Beck et al. 2012; Hess and Beck 2012). Prescribed burning and mechanical treatments such as mowing and pipe harrowing have largely been conducted to reduce the overstory of sagebrush to increase herbaceous understory production (Dahlgren et al. 2006; Davies et al. 2012a, b). Short-term (≤ 10 years) response of forbs to burning or mechanical treatment is generally more positive in mountain big sagebrush (*A. t. Nutt. ssp. vaseyana* [Rydb.] Beetle; Pyle and Crawford 1996; Dahlgren et al. 2006; Van Dyke and Darragh 2006a; but see Nelle et al. 2000) than in Wyoming big sagebrush (*A. t. Nutt. ssp. wyomingensis* Beetle and Young; Wirth and Pyke 2003; Wroblewski and Kauffman 2003; Beck et al. 2009; Davies et al. 2007). Recovery of burned basin (*A. t. tridentata*), mountain, and Wyoming big sagebrush is extremely slow because these species do not resprout after fire (Pechanec et al. 1965; Tisdale and Hironaka 1981). Mowing is an alternative to prescribed burning because it leaves smaller live sagebrush plants after treatment and can be more easily controlled (Davies et al. 2012a). Wyoming big sagebrush canopy cover and volume recover in about 20 years following mowing (Davies et al. 2009), which is much more rapid and less variable than recovery following prescribed burning (Baker 2011).

From 1980 to 2009, USDI-Bureau of Land Management field offices in the Bighorn Basin of north-central, Wyoming USA conducted 156 prescribed burns (100 km²

burned) and 55 mowing treatments (36 km² mowed) in big sagebrush communities used by sage-grouse to reach vegetation management objectives, including enhancing habitat conditions for sage-grouse. Comparison of response variables from mowed and prescribed burned sites provided us a way to compare treatments and assess if either is relatively suitable for enhancing (increase) sage-grouse habitats. Our objective was to evaluate differences between variables reflecting habitat attributes that influence sage-grouse reproduction and survival during nesting and early brood-rearing (hatch to 2 weeks of age; Connelly et al. 2003) within mowed and prescribed burned Wyoming big sagebrush communities. These habitats comprise breeding habitat that Connelly et al. (2000) defined as lek sites, nest sites, and early brood-rearing areas. By comparing response variables between treatments and untreated reference sites, we evaluated whether treatments elicited positive, negative, or neutral responses in forb, insect, and soil parameters related to sage-grouse breeding habitat.

Methods

Study Area

The Bighorn Basin includes Big Horn, Hot Springs, Park, and Washakie counties and encompasses 32,002 km² of north-central Wyoming, USA. The Bighorn Basin is bordered by the Absaroka Range to the west, Beartooth and Pryor Mountains to the north, Bighorn Mountains to the east, and Bridger and Owl Creek Mountains to the south. Sage-grouse occur throughout the Bighorn Basin in areas dominated by big sagebrush (Big Horn Basin Local Sage-Grouse Working Group 2007). The average valley elevation is 1,524 m (1,116 m minimum) and is composed of badland topography and intermittent buttes (Big Horn Basin Local Sage-Grouse Working Group 2007). The Bighorn Basin is semi-arid with the average annual precipitation ranging from 12.7 to 50.8 cm with the greatest precipitation occurring in April and May as rain (Big Horn Basin Local Sage-Grouse Working Group 2007). Dominant land uses in the sagebrush areas between agricultural lands and forested lands in the Bighorn Basin include livestock grazing, bentonite mining, and oil and gas extraction.

Native flora of the Bighorn Basin includes perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), and western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve); shrubs such as Wyoming and mountain big sagebrush, greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), rabbitbrush (*Chrysothamnus* Nutt. spp. and *Ericameria* Nutt.

spp.), and spineless horsebrush (*Tetradymia canescens* DC); and forbs and subshrubs including buckwheat (*Eriogonum* Michx. spp.), desert parsley (*Lomatium* Raf. spp.), milkvetch (*Astragalus* L. spp.), globemallow (*Sphaeralcea* A. St.-Hil. spp.), prairie sagewort (*A. frigida* Willd.), and western yarrow (*Achillea millefolium* L. var. *occidentalis* DC.). Invasive species in the Basin include cheatgrass (*Bromus tectorum* L.), Japanese brome (*B. japonicas* Thunb.), Canada thistle (*Cirsium arvense* [L.] Scop.), hoary cress (*Cardaria draba* [L.] Desv.), and toadflax (*Linaria* spp. Mill.).

Sampling Design

We employed a spatially balanced selection of sampling sites to account for the irregular occurrence of treatments across the Bighorn Basin. To provide a balanced geographic distribution of sampling sites, we used Program S-Draw (Western Ecosystems Technology, Incorporated, Cheyenne, WY, USA), which selects sampling sites using the Universal Transverse Mercator coordinates for each treatment location in a generalized random tessellation-stratified sample. We accordingly selected 25 treated and 25 untreated reference sites for our study. We defined our sampling sites by combinations of soil group, age since treatment by decade (1990–1999 and 2000–2006), and treatment type. For example, sites prescribed burned during 2000–2006 on aridic soils were one of our treatment combinations. We refer to our sample site combinations as chronosequences, which are hypothetical portrayals of soil change as a function of time (Fanning and Fanning 1989). Much of the sage-grouse nesting and early brood-rearing activity in the Bighorn Basin was centered on areas overlying aridic, fine-textured, ustic, and frigid soils, which we used to describe our treatment combinations. We based soil groupings on soil temperature, moisture, and texture, which largely influenced establishment and development of sagebrush communities in the Bighorn Basin (Young et al. 1999).

We randomly selected three treated sites (burned sites $0.4 \pm 0.1 \text{ km}^2$; mowed sites $3.0 \pm 1.0 \text{ km}^2$) from each treatment combination for field sampling in spring 2008. To provide comparative sites, we randomly selected one untreated reference site within a geographic constraint of 0.8 km (mean = 0.4 km) from each randomly selected treated site; however, in four (16 %) instances, we had to compromise our distance criteria to find a nontreated site (range 0.2–1.5 km). Research in Wyoming has shown the majority (64 %) of sage-grouse nesting occurs within 5.0 km of leks in contiguous habitats (Holloran and Anderson 2005). The average distance from the treated and reference sites to the nearest known sage-grouse leks in our study was 4.5 km (range 0.2–11.8 km).

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. To ensure that our data were comparable across years, we sampled the same sites within 1 week in 2008 and 2009. At each selected site, we sampled insect, soil (2009 only), and vegetation parameters from May to July along 3, 100-m transects, extending from N–S. We spaced sample transects 50 m apart starting at a randomly determined point within each treatment and reference site, no closer than 50 m from the nearest untreated edge to avoid edge effects. At sites where sagebrush had been mowed in strips, we placed 1, 100-m transect in three mowed strips at an average spacing of 55 m (range: 32–93 m). We measured response variables related to grouse food forb availability along each of the two, outside 100-m transects, whereas insect abundance and soil parameters were measured along all three transects at each site. We sampled vegetation structural response variables along the middle transect at each site (Hess 2011; Hess and Beck 2012). To avoid trampling vegetation along transects, we collected insect sweep net samples between 2 and 5 m and pitfall samples 5 m west of, but parallel to, each transect, respectively. We used the same protocols to collect forbs and insects at each site once every summer in 2008 and 2009, but only collected soil samples at each site once in summer of 2009.

Food Forb Cover and Nutritional Quality

As a functional group, we sampled canopy cover and nutritional quality of 39 forbs potentially used by grouse (see Hess 2011) during early brood-rearing (late May to mid-June) in $20 \times 50 \text{ cm}$ quadrats. We positioned $20 \times 50 \text{ cm}$ quadrats to the west of each 10-, 20-, 30-, 40-, 50-, 60-, 70-, 80-, 90-, and 100-m mark from the starting point along the outside transects in spring 2008. We positioned $20 \times 50 \text{ cm}$ quadrats to the west of each 5-, 15-, 25-, 35-, 45-, 55-, 65-, 75-, 85-, and 95-m mark of the 100-m transects in spring 2009 to avoid clipping the same location clipped in 2008. In each of the 20 quadrats, we estimated canopy cover of food forbs with the Daubenmire (1959) technique according to seven cover classes: 1 = 0–1 %; 2 = 1–5 %; 3 = 5–25 %; 4 = 25–50 %; 5 = 50–75 %; 6 = 75–95 %; and 7 = > 95 % and used midpoints of these classes to compute food forb canopy cover. We clipped and weighed all perennial food forbs to ground level, initially air dried, followed by oven drying them for 48 h at 60 °C, and then grinding these samples to 1-mm size for gross energy (kcal/kg DM), crude protein (%), calcium (%), and phosphorous (%) analyses (Barnett and Crawford 1994). We combined ground samples across each transect to provide two composited food forb samples

for each treated and reference site; these values were then averaged to provide one estimate for each nutritional value at each site. Samples weighing 2 g were submitted to the Wildlife Habitat and Nutrition Lab at Washington State University, Pullman, Washington, USA for crude protein and gross energy analyses. Calcium and phosphorus were analyzed by dry ashing (Gavlak et al. 2005) at the University of Wyoming Soil Testing Laboratory, Laramie, Wyoming. Nutritional values from these composited forage samples reflected nutrient levels in food forbs found at each site by year.

Insect Abundance

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 ten pitfall traps filled with 95 % propylene glycol (SIERRA antifreeze, Peak Performance Products, Old World Industries, Northbrook, IL, 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 three, 100-m transects. We left covers off pitfall traps from morning to evening of the next day, to capture arthropods during two 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). 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 for each year 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 before 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 allowed us to estimate abundance and biomass for ants, beetles, and grasshoppers at each treatment site.

Indicators of Soil Quality

We collected soil samples from mid-June to early July 2009, 1 m from the outside transects at 20-, 40-, 60-, 80-, and 100-m marks along each of the three, 100-m transects established at each treatment and reference site, yielding 15

soil subsamples per site. We collected soil samples from a depth of 10 cm using a marked hand trowel. We then prepared a single 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 liter of soil for laboratory analyses. We placed all composite samples in labeled plastic bags, air dried them, and stored them until returning from the field. We ground samples with mortar and pestle, sieved them through a 2-mm sieve, and ground them once again. We determined total carbon and total nitrogen content of finely ground subsamples using an ELEMENTAR-automated combustion analyzer (Nelson and Sommers 2001).

Data Analyses

We found no difference (2-sample *t* tests, $P > 0.05$) in any forb, insect, or soil variables that we measured between combinations of fall- and spring-burned treatments, which permitted us to combine these combinations. These considerations gave us six treatment combinations in 2008 and 2009: (1) sites mowed on aridic soils ($n = 3$), (2) sites mowed on ustic soils ($n = 3$), (3) sites prescribed burned during the 1990s on aridic soils ($n = 6$), (4) sites prescribed burned during the 1990s on ustic soils ($n = 6$), (5) sites prescribed burned during 2000–2006 on aridic soils ($n = 3$), and (6) sites prescribed burned during 2000–2006 on ustic soils ($n = 4$).

We analyzed results from our six 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 $Y_{ijk} = \mu + \text{Trt}_i + S_k + \varepsilon_{ijk}$, 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 two treatment means were different (Oehlert 2000). If the null hypothesis was rejected ($P < 0.05$), then 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 with reference sites, (2) prescribed burned sites during the 1990s compared with sites that were prescribed burned during 2000–2006, (3) mowed sites compared with sites that were prescribed burned in the 1990s, (4) mowed sites compared with sites that were prescribed burned during 2000–2006, (5) mowed sites compared with sites that were prescribed burned on aridic soils, and (6) mowed sites compared with 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). Although we report

Table 1 Mean (\pm SE) for insect counts at prescribed burned, mowed, and paired reference sites in the Bighorn Basin, Wyoming, USA, 2008 and 2009

Combination	Year	Ant (no./trap)		Beetle (no./trap)		Grasshopper (no./sweep)	
		Treatment	Reference	Treatment	Reference	Treatment	Reference
Burn							
1990 aridic	2008	2.5 \pm 0.3	2.9 \pm 0.9	1.3 \pm 0.3	1.3 \pm 0.2	4.3 \pm 1.0	1.4 \pm 0.3
	2009	4.3 \pm 1.7	8.3 \pm 3.8	0.7 \pm 0.2	0.9 \pm 0.1	6.2 \pm 2.4	2.1 \pm 0.6
1990 ustic	2008	23.1 \pm 10.6	5.8 \pm 1.7	2.5 \pm 0.9	1.2 \pm 0.3	4.4 \pm 1.0	1.3 \pm 0.2
	2009	18.4 \pm 9.9	10.4 \pm 4.8	1.0 \pm 0.1	0.8 \pm 0.2	3.8 \pm 1.2	1.6 \pm 0.5
2000 aridic	2008	54.0 \pm 19.2	41.1 \pm 19.0	5.5 \pm 3.2	3.2 \pm 0.5	1.5 \pm 0.0	0.2 \pm 0.1
	2009	58.2 \pm 29.1	41.4 \pm 29.0	1.7 \pm 0.3	1.5 \pm 0.5	1.1 \pm 0.3	1.5 \pm 0.4
2000 ustic	2008	14.6 \pm 3.8	25.0 \pm 9.5	2.0 \pm 0.6	2.0 \pm 0.6	2.8 \pm 0.8	2.1 \pm 0.7
	2009	11.9 \pm 5.0	11.4 \pm 8.3	1.3 \pm 0.4	0.7 \pm 0.4	2.7 \pm 1.2	4.6 \pm 2.4
Mow							
Aridic	2008	1.4 \pm 0.2	1.1 \pm 0.1	0.8 \pm 0.2	1.0 \pm 0.5	0.9 \pm 0.6	0.7 \pm 0.5
	2009	20.7 \pm 17.2	4.5 \pm 1.3	1.2 \pm 0.2	1.4 \pm 0.2	1.2 \pm 0.3	1.5 \pm 0.6
Ustic	2008	2.1 \pm 0.3	1.2 \pm 0.3	1.4 \pm 0.4	1.3 \pm 0.4	1.4 \pm 0.4	1.8 \pm 1.1
	2009	39.2 \pm 7.8	11.1 \pm 2.9	1.0 \pm 0.3	1.2 \pm 0.2	2.0 \pm 0.1	1.7 \pm 0.6

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

findings from ten variables in this paper, Bonferroni corrections were based on statistical testing of a larger set of 33 habitat variables collected at each site (see Hess 2011). 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. We performed statistical analyses with the GLM procedure of the Statistical Analysis System (SAS; SAS Institute 2008). We set statistical significance at $\alpha = 0.05$ and report mean and standard errors (SE's) for all estimates.

Results

We sorted, counted, and weighed 6,000 insect subsamples combined into 100 pitfall and 100 sweep net samples to evaluate ant, beetle, and grasshopper counts (Table 1); analyzed 112 food forb subsamples from 100 samples for canopy cover, crude protein, gross energy, calcium, and phosphorus (Table 2); and analyzed 50 soil samples for total carbon and total nitrogen (Table 3). We found no statistical differences in food forb production or weights of ants, beetles, or grasshoppers between treatments or treatments and reference sites, and so these variables are not reported.

Linear Contrasts

We found significant test results for six of our ten variables, we thus only report statistical test results for these six variables, which were significant ($P < 0.008$; Bonferroni correction) in at least one linear contrast comparison (Table 4). Forb characteristics, soil characteristics, and insect counts (except grasshopper counts in 2008), were not

significantly different when examining contrasts between treatments and reference sites (Table 4).

Prescribed burned sites compared with mowed sites in 2008

Ant counts (no./trap) were 18.5 times higher at sites prescribed burned during 2000–2006 versus mowed sites (linear contrast $F_{1, 11} = 14.14$, $P = 0.001$) and 2.5 times higher at sites burned during 2000–2006 versus sites prescribed burned during the 1990s (linear contrast $F_{1, 17} = 8.39$, $P = 0.006$). Beetle counts (no./trap) were 3.2 times higher at sites prescribed burned during 2000–2006 than mowed sites (linear contrast $F_{1, 11} = 8.04$, $P = 0.007$; Table 4). Grasshopper counts (no./sweep) were 4.0 times higher at sites prescribed burned during the 1990s versus mowed sites (linear contrast $F_{1, 16} = 17.91$, $P < 0.001$) and 1.9 times higher at sites burned during the 1990s compared with sites burned during 2000–2006 (linear contrast $F_{1, 17} = 8.99$, $P = 0.005$).

Prescribed burned sites versus mowed sites in 2009

Crude protein (%) in food forbs was 4.4 times higher at sites on ustic soils that were prescribed burned versus mowed (linear contrast $F_{1, 12} = 11.18$, $P = 0.002$; Table 4). Total soil carbon (%) was 3.6 times higher at prescribed burned sites than at mowed sites on aridic soils (linear contrast $F_{1, 11} = 15.09$, $P < 0.001$), 2.9 times higher at sites burned during 2000–2006 than at mowed sites (linear contrast $F_{1, 11} = 28.67$, $P < 0.001$), and 1.5 times higher at sites that were prescribed burned during 2000–2006 than at sites burned during the 1990s (linear contrast $F_{1, 17} = 17.98$, $P < 0.001$; Table 4). Total soil

Table 2 Mean (\pm SE) for food forb canopy cover and nutritional variables at prescribed burned, mowed, and paired reference sites in the Bighorn Basin, Wyoming, USA, 2008 and 2009

Combination	Year	Cover (%)		Calcium (%)		Crude protein (%)		Gross energy (kcal/kg DM)		Phosphorous (%)		
		Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference	
Burn	1990 aridic	2008	3.1 \pm 1.4	2.9 \pm 1.7	1.5 \pm 0.5	1.2 \pm 0.6	10.5 \pm 3.0	7.5 \pm 3.0	4,300.0 \pm 82.6	4,216.0 \pm 64.6	0.3 \pm 0.1	0.2 \pm 0.1
		2009	3.9 \pm 1.0	5.5 \pm 3.2	1.2 \pm 0.3	1.6 \pm 0.7	9.3 \pm 3.6	7.3 \pm 2.3	4,596.0 \pm 110.5	4,362.8 \pm 85.1	0.3 \pm 0.1	0.2 \pm 0.1
	1990 ustic	2008	9.8 \pm 5.0	16.8 \pm 7.7	1.4 \pm 0.4	2.0 \pm 0.5	15.5 \pm 1.1	14.0 \pm 0.6	4,515.6 \pm 105.3	4,270.8 \pm 94.9	0.3 \pm 0.0	0.3 \pm 0.0
		2009	17.7 \pm 8.0	25.4 \pm 9.9	1.1 \pm 0.2	1.7 \pm 0.2	13.6 \pm 2.1	12.8 \pm 1.2	4,546.8 \pm 72.4	4,436.7 \pm 64.0	0.3 \pm 0.0	0.2 \pm 0.0
	2000 aridic	2008	12.1 \pm 4.1	6.2 \pm 1.1	1.8 \pm 0.7	2.2 \pm 1.0	19.3 \pm 5.7	16.2 \pm 4.0	4,547.5 \pm 81.5	4,296.3 \pm 102.8	0.4 \pm 0.2	0.3 \pm 0.1
		2009	22.9 \pm 4.3	13.7 \pm 4.8	2.5 \pm 0.5	2.3 \pm 0.5	12.1 \pm 0.6	14.0 \pm 0.0	4,495.0 \pm 156.0	4,404.0 \pm 61.8	0.3 \pm 0.0	0.2 \pm 0.1
	2000 ustic	2008	4.8 \pm 2.4	3.7 \pm 1.0	1.2 \pm 0.4	1.4 \pm 0.2	16.7 \pm 0.7	17.3 \pm 2.1	4,453.8 \pm 29.4	4,542.0 \pm 92.7	0.3 \pm 0.0	0.3 \pm 0.0
		2009	7.4 \pm 2.5	8.3 \pm 2.1	1.3 \pm 0.3	1.4 \pm 0.3	16.0 \pm 2.3	16.7 \pm 2.1	4,487.4 \pm 81.1	4,560.1 \pm 144.8	0.5 \pm 0.3	0.3 \pm 0.0
	Mow	Aridic	2008	0.6 \pm 0.1	1.8 \pm 0.8	1.1 \pm 0.0	1.4 \pm 0.1	15.2 \pm 9.0	9.8 \pm 6.4	— ^a	— ^a	0.2 \pm 0.1
2009			1.1 \pm 0.5	4.1 \pm 2.6	1.7 \pm 0.4	1.7 \pm 0.6	15.1 \pm 3.4	11.3 \pm 2.2	4,417.7 \pm 178.0	4,486.0 \pm 195.5	0.3 \pm 0.0	0.3 \pm 0.1
Ustic		2008	0.9 \pm 0.2	3.4 \pm 1.7	0.8 \pm 0.5	1.2 \pm 0.6	9.4 \pm 5.0	13.1 \pm 3.7	4,318.0 \pm 0.0	4,475.0 \pm 0.0	0.2 \pm 0.1	0.2 \pm 0.1
		2009	2.0 \pm 0.7	7.2 \pm 2.8	1.8 \pm 0.0	1.7 \pm 0.4	3.3 \pm 5.0	12.1 \pm 3.2	4,064.0 \pm 0.0	4,479.8 \pm 218.3	0.3 \pm 0.1	0.3 \pm 0.0

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

^a Insufficient sample for analysis

Table 3 Mean (\pm SE) for total soil carbon and nitrogen content at prescribed burned, mowed, and paired reference sites in the Bighorn Basin, Wyoming, USA, 2009

Combination	Total carbon (%)		Total nitrogen (%)	
	Treatment	Reference	Treatment	Reference
Burn				
1990 aridic	1.3 \pm 0.3	1.0 \pm 0.2	0.1 \pm 0.0	0.1 \pm 0.0
1990 ustic	2.8 \pm 0.8	2.5 \pm 0.7	0.2 \pm 0.1	0.2 \pm 0.1
2000 aridic	6.3 \pm 0.1	3.1 \pm 1.1	0.5 \pm 0.0	0.3 \pm 0.1
2000 ustic	2.4 \pm 0.3	1.9 \pm 0.4	0.2 \pm 0.0	0.2 \pm 0.0
Mow				
Aridic	0.8 \pm 0.1	0.8 \pm 0.2	0.1 \pm 0.0	0.1 \pm 0.0
Ustic	1.1 \pm 0.3	1.2 \pm 0.4	0.1 \pm 0.0	0.1 \pm 0.0

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

nitrogen (%) was 3.0 times higher at sites that were prescribed burned during 2000–2006 compared with mowed sites (linear contrast $F_{1, 11} = 28.32, P < 0.001$) and 1.5 times higher at sites prescribed burned during 2000–2006

than that during the 1990s (linear contrast $F_{1, 17} = 18.87, P < 0.001$). Total soil nitrogen (%) was also 3.0 times higher at prescribed burned sites on aridic soils compared with mowed sites on aridic soils (linear contrast $F_{1, 11} = 13.88, P = 0.001$; Table 4).

Treatment sites compared with reference sites in 2008

Grasshopper counts (no./sweep) were 2.3 times higher at treatment sites compared with reference sites in 2008 (linear contrast $F_{1, 48} = 8.13, P = 0.007$). Specifically, of the four prescribed burning treatment combinations in 2008, grasshopper abundance was 1.3–7.5-fold higher compared with paired reference sites (Table 1).

Discussion

Through comparing responses at treated sites to those at the reference sites, we found minimal evidence for enhancement of features of sage-grouse breeding habitats following prescribed burning or mowing Wyoming big sagebrush in our study area. Food forb cover and nutritional quality, and total soil carbon and nitrogen, were not enhanced when

Table 4 Linear contrasts for 1990s and 2000s prescribed burned sites, sites mowed during 2000–2006, and untreated reference sites

Habitat variable	Year	Contrast	F_{df}	P	Mean \pm SE	Mean \pm SE
Forbs						
Crude protein (%)	2009	Mow ustic v. burn ustic	11.18 _{1,12}	0.002	3.3 \pm 3.3	14.5 \pm 1.34
Insects						
Beetles (no./trap)	2008	Mow v. 2,000 burns	8.04 _{1,11}	0.007	1.1 \pm 0.2	3.5 \pm 1.4
Ants (no./trap)	2008	Mow v. 2,000 burns	14.14 _{1,11}	0.001	1.7 \pm 0.2	31.5 \pm 11.0
		1,990 burns v. 2,000 burns	8.39 _{1,17}	0.006	12.8 \pm 5.9	31.5 \pm 11.0
Grasshoppers (no./sweep)	2008	Treatment v. reference	8.13 _{1,48}	0.007	3.0 \pm 0.5	1.3 \pm 0.2
		Mow v. 1,990 burns	17.91 _{1,16}	<0.001	1.1 \pm 0.3	4.4 \pm 0.7
		1,990 burns v. 2,000 burns	8.99 _{1,17}	0.005	4.4 \pm 0.7	2.3 \pm 0.5
Soils^a						
Total carbon (%)	2009	Mow aridic v. burn aridic	15.09 _{1,11}	<0.001	0.8 \pm 0.1	2.9 \pm 0.9
		Mow v. 2,000 burns	28.67 _{1,11}	<0.001	1.0 \pm 0.1	2.9 \pm 0.9
Total carbon (%)	2009	1,990 burns v. 2,000 burns	17.98 _{1,17}	<0.001	2.0 \pm 0.5	2.9 \pm 0.9
Total nitrogen (%)	2009	Mow aridic v. burn aridic	13.88 _{1,11}	0.001	0.1 \pm 0.0	0.3 \pm 0.1
		Mow v. 2,000 burns	28.32 _{1,11}	<0.001	0.1 \pm 0.0	0.3 \pm 0.1
		1,990 burns v. 2,000 burns	18.87 _{1,17}	<0.001	0.2 \pm 0.00	0.3 \pm 0.1

Summary of significant ($P < 0.008$; Bonferroni correction) linear contrasts among forb, insect, and soil response variables between prescribed burned, mowed, and reference sites, Bighorn Basin, Wyoming, USA, in 2008 and 2009. Contrasts included (1) treatment compared with reference sites, (2) prescribed burns during the 1990s compared with prescribed burns during 2000–2006, (3) mowed sites compared with prescribed burns during the 1990s, (4) mowed sites compared with prescribed burns during 2000–2006, (5) mowed sites compared with prescribed burned sites on aridic soils, and (6) mowed sites compared with 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 (\pm SE) follows 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)

^a Soil samples were collected only in 2009

comparing mowed or prescribed burned sites with paired reference sites. Even after 9 years of treatment, mowing compared with prescribed burning did not provide higher levels of food forb or insect responses that influence sage-grouse reproduction and survival in breeding habitat. We found higher forb crude protein (burning versus mowed on sites overlying ustic soils), counts of ants and beetles (2000–2006 burns versus mowed sites), grasshopper counts (1990s burns versus mowed sites), and total soil carbon and nitrogen (burning versus mowed at sites overlying aridic soils and 2000–2006 burns versus mowed sites) at prescribed burned sites compared with mowed sites in Wyoming big sagebrush, with some differences related to treatment effects on different soils. Insect counts were not enhanced at mowed compared with reference sites, but grasshopper counts were higher in 2008 at burned sites compared with reference sites.

A short-term increase in forb calcium and protein following prescribed burning in mountain big sagebrush has been reported in Montana (Van Dyke and Darragh 2006b) and Wyoming (Cook et al. 1994), but increased nutritional quality has not been reported in Wyoming big sagebrush following prescribed burning (Rhodes et al. 2010; this study). We found no increase in cover or the nutritional quality (calcium, crude protein, gross energy, or phosphorous) of sage-grouse food forbs following either prescribed burning or mowing, compared with untreated reference sites, in the Bighorn Basin in Wyoming big sagebrush communities. Furthermore, food forb nutritional quality may not have been enhanced because of the lack of soil productivity following treatment. Summers (2005) found no difference in perennial forb cover consisting of residual native and seeded species among Wyoming big sagebrush sites in northern Utah treated with disk plow followed by a land imprinter, 1-way pipe harrow, 2-way pipe harrow, aeration in fall, aeration in spring, and 1-way chaining with an Ely chain compared with nonseeded reference sites. In our study, there was no measurable postburn increase of sage-grouse food forb canopy cover compared with reference sites at 9 or 19 years postburn. This coincides with other research showing no difference among sage-grouse food forb canopy covers between prescribed burned and unburned sage-grouse habitats in Wyoming big sagebrush (Fischer et al. 1996; Wambolt et al. 2001; Beck et al. 2009; Rhodes et al. 2010). Furthermore, research from Oregon has shown that mowing degraded Wyoming big sagebrush communities promotes annual forbs and does not increase perennial forbs (Davies et al. 2012b).

Although abundance of beetles and ants has been found to decline following burning and mowing in mountain (Christiansen 1988) and Wyoming big sagebrush (Rickard 1970; Fischer et al. 1996; Rhodes et al. 2010), we found no difference between ant counts or beetle counts when

comparing prescribed burned or mowed sites to reference sites. Ant and beetle counts at burned sites suggest ant abundance was not adversely affected during 2–19 years postburn in our study area. This finding is similar to a study in southeastern Idaho where ant and beetle abundance increased at 1 year postburn, but returned to preburn levels during 3–5 years postburn in mountain big sagebrush (Nelle et al. 2000). We found greater ant abundance at sites burned during 2000–2006 than at sites mowed during 2000–2006 and at sites burned in the 1990s compared with sites burned during 2000–2006. Rhodes et al. (2010) reported two times the number of grasshoppers in burned sites compared with reference sites in Wyoming big sagebrush in southeastern Oregon. In our study, we found a 2.3-fold increase in grasshoppers at burned sites compared with reference sites during the 2008 field season; however, this difference was not seen during 2009.

For mowed and prescribed burned treatments overlying aridic soils and for mowed sites compared with sites prescribed burned during 2000–2006 total soil nitrogen and soil carbon were 2.9 to 3.6 times higher at prescribed burned sites than at mowed sites (Table 4), but these soil nutrients showed no statistical increase when comparing treatment with reference sites. Similar to our results, Davies et al. (2007) reported no difference in total soil carbon or nitrogen between burned and reference sites in Wyoming big sagebrush in Oregon. Our results, we believe, suggest that mowing did not sufficiently disturb below-ground components to elicit a measurable difference in soil nutrients. In other analyses, we found that although our effect size estimates did not indicate that soil measures increased following treatment, principal components analysis indicated that total soil carbon and nitrogen contents were higher at burned sites compared with those at mowed sites and they were influential in identifying meaningful variables underlying differences among our set of six treatment combinations (Hess 2011).

Conclusions

Our findings are in agreement with a growing body of literature that does not support the use of prescribed fire or mechanical treatments to enhance Wyoming big sagebrush habitats for sage-grouse and other sagebrush-dependent wildlife species (Beck et al. 2009, 2012; Rhodes et al. 2010; Hess and Beck 2012). However, some studies indicate that these same techniques may be more promising in promoting forbs in mountain big sagebrush communities (Pyle and Crawford 1996; Wirth and Pyke 2003; Dahlgren et al. 2006). Our results provide important considerations for practitioners considering burning or mowing to enhance Wyoming big sagebrush communities in the Bighorn Basin and other landscapes under consideration for treatment to enhance

breeding habitat for sage-grouse. Mowing did not increase food forbs or insects on which female and chick sage-grouse rely during nesting or brood-rearing or indicators of soil quality that may promote production of these foods up to 9 years after treatment compared with reference sites or prescribed burned sites. For some treatment combinations and during certain years, prescribed burning showed positive results compared with mowing such as higher ant and beetle counts, forb crude protein, and total soil carbon and nitrogen contents, but all of these characteristics were not enhanced compared with reference sites up to 19 years postburn. **The main benefit of prescribed burning for sage-grouse-breeding habitats was an increase in grasshopper abundance compared with reference sites; however, because grasshoppers are often designated as rangeland pests (e.g., Wyoming Weed and Pest Council 2011), we cannot recommend burning sagebrush to increase grasshoppers for sage-grouse. Furthermore, because burning reduces sagebrush cover and height required by nesting and brood-rearing sage-grouse for long periods, it is not recommended for Wyoming big sagebrush (Hess and Beck 2012). We also cannot recommend mowing to enhance breeding habitat for sage-grouse, because it did not elicit positive changes in food forbs, insects, or indicators of soil quality compared with reference or prescribed burned sites. Other habitat characteristics such as cover and height of perennial grasses were not adversely affected by mowing and prescribed burning Wyoming big sagebrush communities in our study area (Hess 2011; Hess and Beck 2012), suggesting that practitioners must consider how desired characteristics of sage-grouse habitats will respond to treatment objectives. However, mowing Wyoming big sagebrush communities with limited perennial grasses has been shown to increase abundance of exotic annual forbs and grasses, indicating the need to avoid mowing-degraded communities (Davies et al. 2012b).**

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