

Winter foraging ecology of Greater Sage-Grouse in a post-fire landscape

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ABSTRACT

In the Great Basin, changes in climate and associated fire regimes may alter the density and distribution of shrubs, changing the structure and diet quality of plants in burned areas. We evaluated how the structural and phytochemical characteristics of three-tip sagebrush (*Artemisia tripartita*) relative to Wyoming big sagebrush (*A. tridentata wyomingensis*) influence the winter foraging ecology of Greater Sage-Grouse (*Centrocercus urophasianus*) at a site with a known history of fire in south-central Idaho. Three-tip sagebrush had lower protein content and lower chemical defenses compared to Wyoming big sagebrush. We found that time since last fire over a 30-year history was more strongly correlated with changes in phytochemicals in three-tip sagebrush compared to Wyoming big sagebrush. Despite phytochemical differences, both Wyoming big sagebrush and three-tip sagebrush were browsed relative to their availability. However, within a species, smaller plant height and lower concentrations of phytochemicals, specifically two individual monoterpenes, explained diet selection by sage-grouse. Our results indicate that dietary quality of three-tip sagebrush may provide acceptable forage for sage-grouse in post-fire landscapes where other species of sagebrush have not yet recovered. However, relying on re-establishment of one species of sagebrush without consideration of structural and dietary quality may compromise successful conservation efforts.

1. Introduction

Wildfires are becoming increasingly common in western North America. Coupled with conversion to invasive annual grasses, fires are threatening large expanses of shrubland landscapes. The natural fire regime in sagebrush (*Artemisia* sp.) landscapes has been altered by invasion of annual grasses resulting in the loss of approximately 11% of available sagebrush over the last 30 years (Brooks et al., 2015). The impact of fire on sagebrush communities contributes to the current and projected long-term declines of Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter, sage-grouse; Connelly et al., 2000a; Beck et al., 2009; Rhodes et al., 2010; Lockyer et al., 2015; Coates et al., 2016).

Both mountain big sagebrush (*A. tridentata vaseyana*) and Wyoming big sagebrush (*A. t. wyomingensis*) do not meet sage-grouse habitat guidelines (Connelly et al., 2000b) for more than twenty years after being burned with only 2% of post-fire restoration sites meeting winter habitat guidelines within 20 years (Arkle et al., 2014). Specifically, Wyoming big sagebrush may take 100 or more years to recover to pre-fire canopy cover after disturbance (Nelle et al., 2000; Baker, 2006; Beck et al., 2009; Rhodes et al., 2010; Arkle et al., 2014). The long-term

losses of sagebrush cover after fires may explain reduced nesting success and survival of sage-grouse using burned areas (Foster et al., 2018), decreased lek attendance (Connelly et al., 2000a), and decreased population sizes (Coates et al., 2016; Smith and Beck, 2018).

Fires may reduce availability and quality of sagebrush directly through mortality (Baker, 2006) or indirectly by altering sagebrush communities due to variable responses of plant species to fire (Passey and Hugie, 1962; Lesica et al., 2007; Beck et al., 2009). For example, three-tip sagebrush (*A. tripartita*) recovers twice as fast as Wyoming big sagebrush species after fires (Beck et al., 2009) because plants can resprout instead of re-establishing from seed (Passey and Hugie, 1962; Lesica et al., 2007). Although three-tip sagebrush currently has a relatively small range (Tirmenstein, 1999) compared to big sagebrush taxa, populations of three-tip sagebrush are expected to expand throughout the West due to both decreased fire return intervals (Baker, 2006) and increased temperature (Dalgleish et al., 2011). Expansion of three-tip sagebrush may influence sage-grouse populations. For example, sage-grouse used three-tip sagebrush for nesting cover less than expected based on availability in south-central Idaho, and had lower nesting success under three-tip sagebrush than birds nesting under sympatric

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Wyoming big sagebrush (Lowe et al., 2009).

Sage-grouse have strong site fidelity, and therefore may continue to use sub-optimal habitat after fires rather than altering patterns of habitat use. The lack of behavioral plasticity in sage-grouse and high site fidelity (Berry and Eng, 1985), coupled with slow recovery of sagebrush (Baker, 2006; Beck et al., 2009), ineffective restoration of sagebrush communities (Nelle et al., 2000; Arkle et al., 2014), and changes in shrub composition (Beck et al., 2009, 2012) may explain reduced nest success and survival of individual sage-grouse (Foster et al., 2018) and overall reductions in population size (Smith and Beck, 2018) in post-burn habitats.

In addition to changes in cover and composition of shrubs that provide critical hiding cover, wildfires may also alter food availability and food quality. Importantly, higher quality diets are correlated with higher nutritional condition and reproductive success for many species of herbivores (Moss and Watson, 1984; Gregg et al., 1994; DeGabriel et al., 2009; Wing and Messmer, 2016). Diet quality is therefore an important consideration in understanding population changes in sage-grouse following large-scale wildfires in winter habitat. Fires may alter the dietary quality of sagebrush present in post-burn habitats through changes in the availability of species that vary in phytochemistry (i.e., three-tip sagebrush versus Wyoming big sagebrush). In addition, fires can alter protein content (DeWitt and Derby, 1955) and concentrations of plant secondary metabolites (PSMs) within a species as plants resprout or grow from seeds (Campbell and Taylor, 2007; Bryant et al., 2009). For example, birch trees (*Betula* sp.) produce more PSMs in areas with greater fire frequencies and higher percent area burned than adjacent areas (Bryant et al., 2009). Because sage-grouse depend on sagebrush for cover and food, both the structural and dietary quality of sagebrush species that remain or are recruited after fires are important for understanding demographic consequences for sage-grouse in post-burn landscapes.

Our overall objective was to examine factors that influence habitat use and diet selection by sage-grouse inhabiting a post-fire landscape dominated by Wyoming big sagebrush and three-tip sagebrush. First, we predicted that three-tip sagebrush would generally be higher in crude protein and PSMs and that these phytochemicals would be influenced more by fire history than Wyoming big sagebrush because three-tip sagebrush has a greater ability to regrow following fires (Passey and Hugie, 1962). Second, we predicted that sage-grouse would select plants and plots with medium heights (25–35 cm) and moderate cover (10–30%) because of the importance of cover for sage-grouse using winter habitats (Beck, 1977; Connelly et al., 2000b; Carpenter et al., 2010; Smith et al., 2014; Holloran et al., 2015). Finally, we predicted that sage-grouse would select species, plots, and individual plants of sagebrush with the highest crude protein and lowest concentrations of PSMs because diet selection by sage-grouse in winter is driven by phytochemicals at different spatial scales (Frye et al., 2013; Remington and Braun, 1985).

2. Methods and materials

2.1. Study area

We conducted fieldwork in south-central Idaho during January 2014 in Power, Blaine, and Minidoka counties (42.958690 N, –113.398059 W). Elevations at our study area range from 1300 m to 1650 m. Average snow depth during our fieldwork did not exceed 6 cm. Although the study area had relatively sparse sagebrush cover (average $\pm$ SEM: $7.8 \pm 6.3\%$) following frequent wildfires for the last three decades (see Fig. S1 in Supplemental Information, available online) it was dominated by Wyoming big sagebrush (5% cover) and three-tip sagebrush (2% cover). The study area was also characterized by widespread cover of cheatgrass (*Bromus tectorum*) and crested wheatgrass (*Agropyron cristatum*), with invasive grasses occurring at 97% (31/32) of plots.

2.2. Field methods

The Idaho Department of Fish and Game (IDFG) captured and marked 23 sage-grouse (13 males, 10 female) with radio-transmitters and leg bands using standard capture and marking techniques and following approved protocols (Boise State University Institutional Animal Care and Use Committee permit #006-AC11-003 and #006-AC13-010 and Idaho Fish and Game permit #110914). Sage-grouse were trapped February through April 2013 using spotlights at night and a long-handled net (Geisen et al., 1982; Wakkinen et al., 1992). Birds were weighed, measured, and fitted with aluminum leg bands and 14–15 g necklace-style very-high frequency (VHF) radio-transmitter collars from Advanced Telemetry Systems, Inc. (ATS model # A4050; 470 First Ave. NW, Isanti, MN 55040), designed for sage-grouse. Birds were released at the site of capture.

Radio-marked sage-grouse were flushed from foraging plots ($n = 16$) during the daytime during January 2014 (hereafter, used plots). Used plots were those plots of sagebrush where fresh signs of foraging by sage-grouse could be identified (scat, tracks, bite marks) and where observers witnessed sage-grouse flush, using radio-marked birds or from flocks that were flushed by chance. The group foraging behavior of flocks and inability to directly observe the radio-marked sage-grouse within a used plot before flushing prevent us from directly linking characteristics of the used plot to an individual bird. In addition, used plot included those where we flushed birds opportunistically and did not detect any of the radio frequencies of our radio-marked birds ($n = 6$ used plots). After flocks (ranging from 1 to 13 individuals) were flushed, the used plots were delineated using tracks (if snow was present) and fresh fecal pellets. The highest concentration of tracks or fresh pellets was used to estimate the center of the plot. Radiating out of the center of each used plot, we located plants that were fed on by the flock that was flushed. Browsed plants were indicated by bright green meristematic tissue from bite marks on leaves (Remington and Braun, 1985; Frye et al., 2013; Wing and Messmer, 2016).

We also generated a set of random coordinates constrained within the study area boundary using ArcGIS (Environmental Systems Research Inc., Redlands, CA, USA). The boundary the study area was determined from locations of radio-marked sage-grouse collected from fixed wing flights performed by IDFG from December through February the previous year. Each random plot ($n = 16$) was paired temporally and spatially to a used plot to minimize confounding factors of time (Kelsey et al., 1982) when comparing structural characteristics and diet quality between used plots and random plots that were available across the study area. The random plot closest to the used plot was selected and sampled on the same day as each used plot. Used and random plots were not discrete units of sagebrush, but were defined by the center of foraging activity by sage-grouse (used plots) or proximity to the random coordinate used as the center of random plots (random plots).

We collected branches from plants (plants > 15 cm tall) or entire plants (plants < 15 cm tall) within an approximate 10-m radius of the center of each plot at geographically and temporally paired used and random plots on the same day. At each used plot, sagebrush leaves were collected from three randomly selected plants that were freshly browsed by flushed sage-grouse and three randomly selected non-browsed plants for each species of sagebrush present within the plot. Plant samples were pooled for analyses by combining equal amounts of biomass from each plant. This was done because spatial autocorrelation of plants in close proximity (Moore et al., 2010) results in non-independent samples. At each random plot, we searched for plants with fresh browse. If browsing was present (1 of 16 random plots contained browsed plants), samples of both browsed and non-browsed plants were collected. This plot was still considered a random plot because it represented the foraging resources available to foraging sage-grouse on the landscape, which may include non-browsed plots, recently browsed plots, and plots that had been browsed sometime within the last year. If browsing was not present, we collected samples from three randomly

selected sagebrush plants of each species present within the plot.

Browsed plants had a minimum of ten fresh bite marks by sage-grouse. Non-browsed plants were those with no more than one bite mark by sage-grouse. Non-browsed plants had evidence of sage-grouse presence (tracks, droppings, or other browsed plants) within 1 m of each plant (Frye et al., 2013) to ensure that non-browsed plants within used plots could have been encountered by sage-grouse, but were not selected.

Sagebrush species were identified in the field using morphological characteristics and species identification was verified using unique chemical profiles. Leaf samples were kept on ice in the field and transferred to a -20°C freezer in the laboratory to prevent volatilization of monoterpenes. Laboratory analyses of diet quality were conducted within one year of sample collection.

Average snow depth was recorded at each plot at the time of collection, as snow cover can influence resource availability (Beck, 1977; Carpenter et al., 2010). We averaged snow depth measured at five random points within the plot. Slope, aspect, and elevation were recorded using a clinometer, compass, and global positioning system (GPS) unit, respectively.

2.3. Structural characteristics

We measured plant density, canopy cover, height, and biomass per bite as the structural characteristics of each species at a plot scale (plant density, canopy cover, average height) and at a plant scale (height, biomass per bite). Density, canopy cover, height (above snow, if present) were measured along two perpendicular 20-m transects at each plot.

We measured leaf biomass per bite for approximately 20 plants for each species of sagebrush. Biomass per bite was estimated by clipping leaves off each plant that mimicked bite marks observed on plants freshly browsed by sage-grouse. Clipped leaves were weighed on an analytical balance (resolution of 0.0001g) after drying to assess the average biomass (g dry weight, DW) consumed per bite. We estimated the concentration of crude protein, total monoterpenes, phenolics, and coumarins consumed per bite as the product of biomass per bite and the average concentration of protein or PSM for each species.

Fire history was a continuous numeric variable, calculated as the number of years since the most recent fire (range = 3–31 years since most recent fire). Fire location and date throughout the study area were compiled into spatially explicit polygons by the Bureau of Land Management and archived at the Interactive Numeric & Spatial Information Data Engine (INSIDE) Idaho spatial data clearinghouse (Knauth, 2015). We extracted the historic fire data in ArcGIS from the “fire perimeters historic” shapefile from the INSIDE Idaho spatial data clearinghouse (Knauth, 2015).

2.4. Dietary characteristics

We measured crude protein (% dry weight (DW)), total, individual, and diversity of monoterpenes, phenolics, and coumarins (a subclass of phenolics) on a per-gram and per-bite basis to represent the dietary characteristics of each species. Because sage-grouse pluck leaves instead of eating whole stems (Remington and Braun, 1985; Frye et al., 2013), only leaves were used for laboratory analysis. Leaves were removed from stems by dipping samples into liquid nitrogen and brushing leaves off the stems into a beaker. We ground leaf samples with a mortar and pestle in liquid nitrogen to a sample size of approximately 2 mm. Ground leaves were weighed into separate vials for analysis and samples were stored at -20°C until chemical analyses were conducted. Crude protein (% of DW) was analyzed at Dairy One Forage Laboratory (730 Warren Road, Ithaca, NY 14850, USA) using combustion methods on 0.5–1.0 g DW of each sample.

We used a gas chromatograph (GC; Agilent Technologies Agilent 6890N; 5301 Stevens Creek Boulevard, Santa Clara, CA 95051, USA)

with a headspace auto-sampler (Hewlett-Packard HP7694; 1501 Page Mill Road, Palo Alto, CA 94204, USA) to detect monoterpenes in leaf samples. A 100-mg (wet weight, WW) subsample of ground leaves were measured immediately after grinding into a 20-ml gas chromatography headspace vial. We identified compounds using a cocktail of monoterpene standards to generate reference retention times (min). Not all compounds could be identified and unknown compounds were labeled based on retention times. Retention times and peak areas (area under the curve, AUC) were calculated using Hewlett-Packard ChemStation version B.01.00 (Agilent Technologies). Headspace and gas chromatograph settings and operating conditions are detailed in the Supplemental Information, available online.

We calculated chemical diversity by applying the Shannon index equation, $H = -\sum p_i (\ln p_i)$ where H = chemical diversity, and p_i is the concentration of an individual compound. (MacArthur, 1965). We applied this equation to the major monoterpene compounds (compounds with an AUC > 1% of the total AUC in $\geq 70\%$ of samples within a species, and retention time < 24 min). After analysis, samples were dried in a 60°C oven for 48 h and re-weighed to calculate the DW.

Phenolics and coumarin concentrations were assessed using colorimetric assays. Samples (50 mg WW) were extracted for two 3-min periods in 1.0 ml of GC-grade methanol in a sonicating water bath and filtered through glass wool. We used an adapted Folin-Ciocalteu assay (Frye et al., 2013) to measure phenolics, where samples were diluted with methanol to fit within the standard curve. Gallic acid (# 92-6-15, Acros Organics/Thermo Fisher Scientific, 2000 Park Lane Drive, Pittsburgh, PA 15275, USA) diluted in methanol was used as a standard (0–2900 μM). For each sample, 20 μl of the diluted extract was pipetted in triplicate into 96-well plates. Next, we added 100 μl of 10% Folin-Ciocalteu reagent to each well, mixed gently, and then added and mixed 80 μl of 700 mM (7.5%) sodium carbonate. Plates were incubated at room temperature for 2 h, and then were shaken on the plate reader for 60 s before reading. We measured color intensity using a BioTek Synergy MX multi-mode plate reader (BioTek, Winooski, VT, USA) at an absorbance of 765 nm at room temperature.

For the coumarin assay, 50- μl subsamples of extracts were pipetted into a 96-well plate in triplicate. We measured color intensity at an absorbance of 350 nm excitation and 460 nm emission at room temperature. We used scopoletin (# 5995-86-8, Acros Organics) diluted in methanol as a standard (0–80 μM).

2.5. Statistical methods

We used JMP Pro 11.0 (SAS Institute Inc., Cary, NC, USA) or R version 3.2.3 (www.r-project.org, accessed 12 October 2015) for all statistical analyses. Values are reported as mean $\pm$ SEM, and p-values of 0.05 were considered significant.

Differences between species.— To assess structural differences, we compared density, canopy cover (%), height (cm), and biomass per bite (g DW/bite) between sagebrush species using analysis of variance (ANOVA) for the normally distributed parameters. To assess dietary differences (non-parametric distributions for at least one species), we compared dietary quality of each species through non-parametric univariate comparisons (where $\alpha = 0.05$). We used a Kruskal-Wallis test with a normal approximation to compare percent crude protein (% of DW), total monoterpene concentration and individual monoterpene concentrations (AUC/100 μg DW), total number of major monoterpene compounds, monoterpene diversity (Shannon index), phenolics (μmol of gallic acid equivalents/g DW), and coumarin (μmol of scopoletin equivalents/g DW) concentration between all (average browsed and non-browsed in used and random plots) three-tip sagebrush and all Wyoming big sagebrush. We focused on these larger classes of phytochemicals to assess selection based on benefit (crude protein) or cost (classes of PSMs) per effort expended (bite) by sage-grouse.

Influence of fire on structure and dietary quality.— We used linear and non-linear (polynomial) regressions to test the influence of fire (years

since the most recently documented fire) on structural and dietary parameters independently for each species of sagebrush at the plot scale. We tested the following measures as response variables for each type of model: density, percent cover, height, crude protein, total and individual monoterpenes, phenolics, and coumarins of each species within a plot. For each response variable, we compared model structures using Akaike's Information Criterion values with a sample size bias-adjustment (AIC_c) to select the best model for that response variable. These parameters were selected based on the previously documented responses of these variables to fires (Jakubas et al., 1994; Greene et al., 2012). Additionally, we used a Wilcoxon test to evaluate if used and available plots had different fire histories.

Selection for species of sagebrush.— To assess selection for species at the landscape-scale, we used contingency analyses to compare the availability of each species of sagebrush at used and random plots. The landscape scale is a summary of species present within each plot across the entire study area, and represents the broad-scale availability of each species of sagebrush throughout the study area. Random plots were considered to be the expected (available) frequency, and used plots were considered the observed frequency of plot use. To assess relative intake between browsed species at the plot scale, we used a non-parametric Kruskal-Wallis test with a normal approximation to compare the average number of bites per browsed plant (browse intensity) within a used plot.

Selection at plot- and plant-scales.— Due to large number of variables that differed between species (Table 1), diet selection at the plot scale was analyzed for each species separately. The plot scale is an average of

the browsed and non-browsed plants within any used or random plot, and represents the foraging resources and hiding cover available for sage-grouse to use during their daily foraging activities. To address multicollinearity, we tested plant density, height, percent cover, crude protein, individual monoterpenes, phenolics, and coumarins for correlations. We removed correlated variables ($|r| > 0.7$) within each species, and remaining variables were used to build models. Dietary variables were selected if they represented a unique chemical class (e.g., protein, monoterpenes, phenolics, coumarins), were present in both species of sagebrush, could be identified using chemical standards, or were compounds that had higher concentrations than other correlated variables.

Selection at the plot scale was evaluated using a logistic regression where plot use (used or random) was the binary response and continuous predictors included structural (density, percent cover, height, fire history) and dietary (protein, monoterpenes, phenolics, and coumarins) parameters. Models were compared to one another and to a null (intercept-only) model using information-theoretic methods, for each species separately and for both species averaged in mixed plots. We used AIC_c for each predictor variable, with results detailed in Supplemental Information, available online. We calculated odds ratios to predict the odds of use for models within 2 AIC_c units from the top model (i.e. $\Delta AIC_c < 2$) in each predictor category (structural, nutrient, and dietary).

The plant scale was a comparison between browsed and non-browsed plants occurring within a foraging plot, representing selection of individual plants for foraging resources within a used plot. Selection

Table 1

Mean (95% confidence interval) concentrations for structure (density, % cover, height, biomass per bite), nutrient content (% crude protein), and plant secondary metabolites (total, individual, and diversity of monoterpenes, phenolics, and coumarins) in Wyoming big sagebrush (*Artemisia tridentata wyomingensis*, ATW, n = 65) and three-tip sagebrush (*A. tripartita*, AT, n = 28) in south-central Idaho, USA during January 2014. Retention times used to identify compounds are shown for monoterpenes.

Parameter	Retention time (minutes)	Value in ATW	Value in AT
Density (plot) ^a	NA	0.597 (0.360–0.833)	0.532 (0.093–0.973)
Percent cover (plot) ^b	NA	6.0 (4.0–8.0)	4.4 (0.8–8.1)
Height ^c	NA	52.22 (45.77–58.67)	29.09 (24.06–34.11)
Crude protein ^d	NA	13.26 (12.83–13.71)	10.31 (9.65–10.97)
Total monoterpenes ^e	NA	67.69 (63.56–71.83)	99.45 (91.67–107.42)
Unknown 3.2 ^e	3.2	27.02 (24.77–29.26)	15.18 (10.36–20.00)
Unknown 3.6 ^e	3.6	7.30 (6.22–8.37)	— ⁱ
Unknown 11.9 ^e	11.9	8.00 (5.44–10.56)	— ⁱ
Unknown 12.4 ^e	12.4	2.13 (1.45–2.80)	10.45 (9.27–11.63)
α -pinene ^e	12.9	0.48 (0.21–0.77)	6.64 (5.59–7.68)
Camphene ^e	13.5	2.57 (2.01–3.41)	16.87 (14.35–19.39)
β -pinene ^e	14.6	4.89 (3.47–6.31)	2.37 (0.72–4.00)
α -phellendrine ^e	15.6	2.81 (2.33–3.27)	— ⁱ
ρ -cymene ^e	16.4	5.30 (3.91–6.68)	35.34 (31.68–39.00)
1,8-cineole ^e	16.7	3.71 (2.45–4.95)	0.97 (0.49–1.45)
Unknown 18.2 ^e	18.2	5.34 (4.47–6.02)	— ⁱ
Unknown 18.6 ^e	18.6	12.17 (9.97–14.38)	4.67 (0.23–9.10)
Unknown 20.5 ^e	20.5	1.74 (1.13–2.36)	— ⁱ
Camphor ^e	20.7	7.88 (6.61–9.16)	— ⁱ
Unknown 21.0 ^e	21.0	1.76 (1.48–2.04)	54.28 (43.80–64.76)
Unknown 21.5 ^e	21.5	9.62 (6.71–12.52)	1.58 (1.30–1.86)
Unknown 23.5 ^e	23.5	6.63 (4.12–9.14)	— ⁱ
Number compounds ^f	NA	13.03 (12.33–13.72)	8.50 (7.62–9.37)
Monoterpene diversity ^g	NA	1.95 (1.88–2.01)	1.26 (1.18–1.34)
Phenolics ^h	NA	2975 (2595–3356)	2128 (1703–2553)
Total coumarins ^h	NA	3.16 (1.75–4.56)	4.48 (0.79–8.17)

^a Density of sagebrush plants (plants/m²) analyzed at plot only.

^b Percent cover of sagebrush plants, calculated from canopy gap measures (%) analyzed at plot only.

^c Height (cm).

^d Crude protein (% dry weight [DW]).

^e Monoterpenes, concentration in AUC/100 μ g DW, with retention times of individual monoterpenes shown in the second column.

^f Total number of monoterpenes with retention times < 24 min, > 1% total AUC, and present in > 70% of samples within each taxa.

^g Monoterpene diversity calculated as a Shannon Index, incorporating evenness and abundance of major compounds.

^h Phenolics and coumarins, concentration in μ mol of gallic acid (phenolics) or scopoletin (coumarins) equivalents/g DW.

ⁱ Indicates a monoterpene that was not detected for that species.

at the plant scale within each species was evaluated with conditional logistic regressions (Hosmer and Lemeshow, 1985), where plant type (browsed or non-browsed) was the binary response and the continuous predictors were structural or dietary variables. Models were stratified by plot. Models were compared to one another and to a null model using AIC_c for each species separately. Parameters from models with 85% confidence intervals overlapping 1 were not considered reliable to estimate the odds of plot or plant use.

Intensity of use among browsed plants.— We also tested if any predictor variable selected for the plant-scale analysis (structural or dietary variables) predicted the intensity of use (number of bite marks) on each browsed plant. Linear models were fitted for each predictor and were compared to one another using AIC_c for each species separately. Parameters from models with 95% confidence intervals overlapping zero were not considered to influence browse intensity.

3. Results

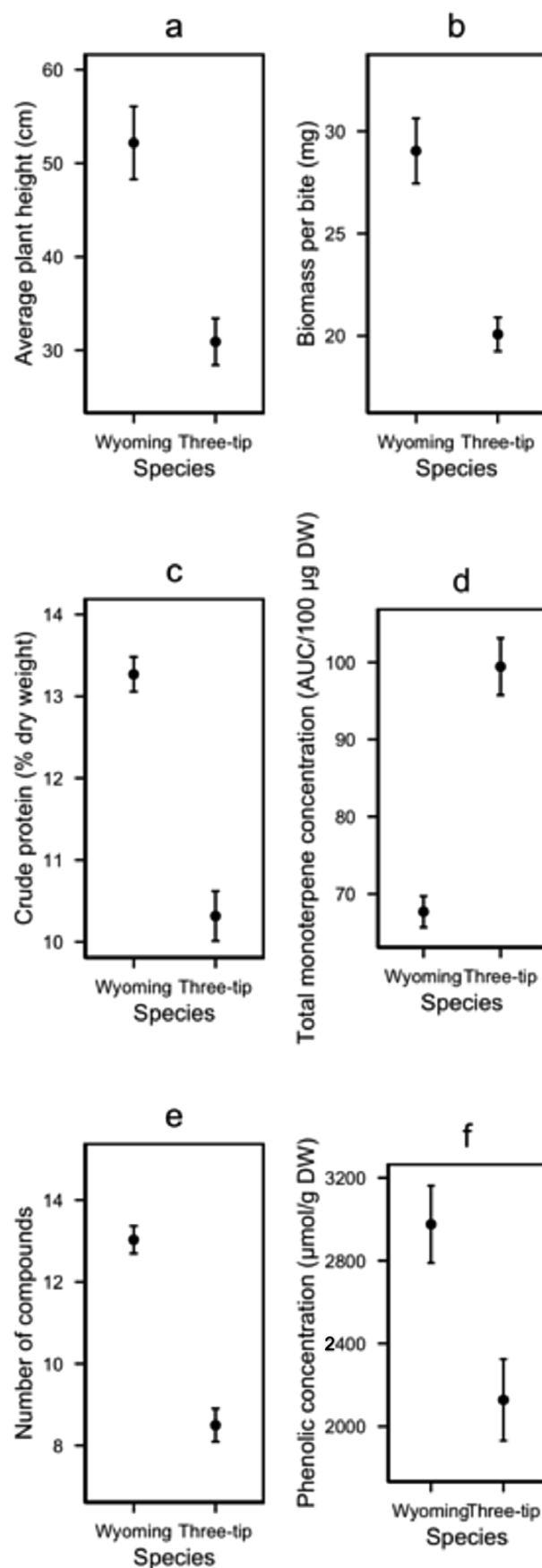
We flushed flocks from 16 used plots and collected plants at those 16 used plots with 16 temporally and spatially paired random plots. Flocks ranged in size from 1 to 13 individuals (average = 4.3 birds), and birds flushed from an estimated 10–75 m from the observer (average = 26 m) and were observed in the plot where bite marks were observed. Given the average flush distance, we were reasonably certain that the fresh bite marks and fresh fecal pellets were produced by the flock that had been flushed.

3.1. Species comparisons across landscape

Structural differences between species.— Overall, Wyoming big sagebrush was more available than three-tip sagebrush across the landscape, as assessed using the proportion of plots with each species of sagebrush present within the plot. Wyoming big sagebrush was the only species available at 50% of plots, three-tip sagebrush was the only species available at 6% of plots, and the remaining plots (44%) had both species of sagebrush present (hereafter, mixed) with similar plant density and similar percent cover of each species within these mixed plots (Table 1). Wyoming big sagebrush was 1.8 times taller than three-tip sagebrush ($F_{1,92} = -3.331$, $P < 0.001$; Fig. 1, Table 1). The branching morphology of both species allows for leaves to grow low enough to the ground to be accessible to a foraging sage-grouse. The biomass per bite of Wyoming big sagebrush was approximately 1.4 times larger than in three-tip sagebrush ($F_{1,36} = 27.167$, $P < 0.001$; Fig. 1, Table 2).

Dietary differences between species.— In general, Wyoming big sagebrush was higher in crude protein ($F_{1,92} = -4.796$, $P < 0.001$), lower in total monoterpenes ($F_{1,92} = 4.820$, $P < 0.001$), and had higher diversity of monoterpenes ($F_{1,92} = -7.149$, $P < 0.001$). Additionally, seven monoterpenes were only detected in Wyoming big sagebrush (Fig. 2). Wyoming big sagebrush also had higher phenolics compared to three-tip sagebrush ($F_{1,92} = -3.178$, $P = 0.002$; Table 1, Fig. 1; Figs. S3 and S4, and Table S1, available online in Supporting Information). Wyoming big sagebrush had 2.0 times higher average crude protein per bite ($F_{1,36} = 89.858$, $P < 0.001$) and 10 times higher average phenolics per bite than three-tip sagebrush ($F_{1,36} = 304.591$, $P < 0.001$; Table 2). There was no difference in the average concentrations of total monoterpenes per bite ($F_{1,36} = 0.974$, $P = 0.331$).

Influence of fire on structure and dietary quality.— Fire history (years since most recent fire) did not explain structural parameters (total percent cover, density, and average height above snow) for Wyoming big sagebrush, but percent cover of three-tip sagebrush increased over time since last fire ($F_{3,9} = 19.92$, $P < 0.001$). In Wyoming big sagebrush plants, monoterpene Unknown 21.5 min showed a decline over a 30-year period after fires ($F_{2,60} = 3.855$, $P = 0.027$). In three-tip sagebrush, total monoterpenes ($F_{2,24} = 6.143$, $P = 0.007$) and camphene ($F_{2,24} = 9.445$, $P = 0.001$) declined in concentration over a 30-year



(caption on next page)

Fig. 1. Mean $\pm$ SEM structural and phytochemical parameters for sagebrush samples collected at Greater Sage-Grouse (*Centrocercus urophasianus*) foraging plots and random plots in Idaho. Samples were collected in January 2014 for Wyoming big sagebrush (*Artemisia tridentata wyomingensis*, $n = 63$) and three-tip sagebrush (*Artemisia tripartita*, $n = 27$). Differing parameters include: (a) height (cm), (b) biomass per bite (mg dry weight [DW] per bite), (c) crude protein (% DW), (d) total monoterpene concentrations (AUC/100 μ g DW), (e) number of monoterpene compounds with retention times < 24 min and AUC > 1% of total AUC, and (f) total phenolic concentrations (μ mol gallic acid equivalents/g DW; Table 1).

Table 2

Mean (95% confidence interval) values for concentrations of crude protein or PSMs per bite and intensity of use of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*, ATW, $n = 17$) or three-tip sagebrush (*A. tripartita*, AT, $n = 20$) browsed by Greater Sage-Grouse (*Centrocercus urophasianus*) during January 2014 in south-central Idaho, USA.

Parameter	Value in ATW	Value in AT
Biomass per bite ^a	29.0 (25.9–32.3)	20.2 (18.6–21.8)
Crude protein per bite ^b	0.431 (0.381–0.481)	0.207 (0.189–0.225)
Total monoterpenes per bite ^c	18.86 (16.43–21.28)	20.27 (18.40–22.14)
Phenolics per bite ^d	0.608 (0.537–0.679)	0.068 (0.060–0.075)
Total coumarins per bite ^d	0.107 (0.095–0.120)	0.121 (0.111–0.131)
Intensity of use ^e	11.52 (6.60–16.44)	14.31 (3.97–26.65)

^a Biomass per bite in mg dry weight (DW)/bite.

^b Crude protein per bite in %/bite.

^c Total monoterpenes per bite in AUC/100 μ g/bite.

^d Phenolics and total coumarins in μ mol of gallic acid (phenolics) or scopoletin (coumarins) equivalents/g DW/bite.

^e Intensity of use is the number of fresh bite marks by Greater Sage-Grouse per plant.

period after a fire. In contrast, concentrations of crude protein ($F_{2,24} = 27.24$, $P < 0.001$) and chemical diversity ($F_{3,23} = 9.038$, $P < 0.001$) increased over a 30-year prior after fires in three-tip sagebrush. The median time since fire was significantly longer in used plots was (13.5 years) compared to random plots (9.3 years; $W = 70$, $p = 0.0001$).

3.2. Multi-scale selection of structural and dietary characteristics

Selection for species.— Sage-grouse selected Wyoming big sagebrush and three-tip sagebrush in proportion to their availability (Table 3; Chi-squared: $\chi^2(2, n = 32) = 1.286$, $P = 0.526$). The number of bite marks by sage-grouse per browsed plant within a used plot did not differ between species (Table 2).

Selection at the plot scale.— Total sagebrush density did not differ between used (0.7 ± 0.2 plants/m²) and random plots (0.9 ± 0.2 plants/m²; $F_{1,30} = 0.705$, $P = 0.408$). However, total percent sagebrush cover was nearly half as low at used ($5.6 \pm 4.6\%$) compared to random plots ($10.0 \pm 1.8\%$; $F_{1,30} = 4.3282$, $P = 0.046$).

Several factors explained plot scale selection by sage-grouse within each sagebrush species. For Wyoming big sagebrush, plant height was the top predictor of use (lowest AIC_c value), but concentration of unknown monoterpene 21.0 was also a top model explaining selection of plots by sage-grouse (Table 4; Fig. 3). Probability of use of a plot declined by a factor of 0.92 for every 1 cm increase in plant height. Probability of use of a plot declined by a factor of 0.40 for every 1 AUC/100 μ g DW increase in monoterpene Unknown 21.0. For three-tip sagebrush, the average concentration of β -pinene (AUC/100 μ g DW) was the top predictor of use (lowest AIC_c value). Concentration of phenolics, fire history (years since most recent fire), and plant height also explained selection of plots (Table 4; Fig. 4), but all had 85% confidence intervals that overlapped 1 (Table 4), indicating parameters were unreliable for predicting odds of use. Probability of use of a plot increased by a factor of 1.007 for every 1 μ mol/g DW increase in concentration of

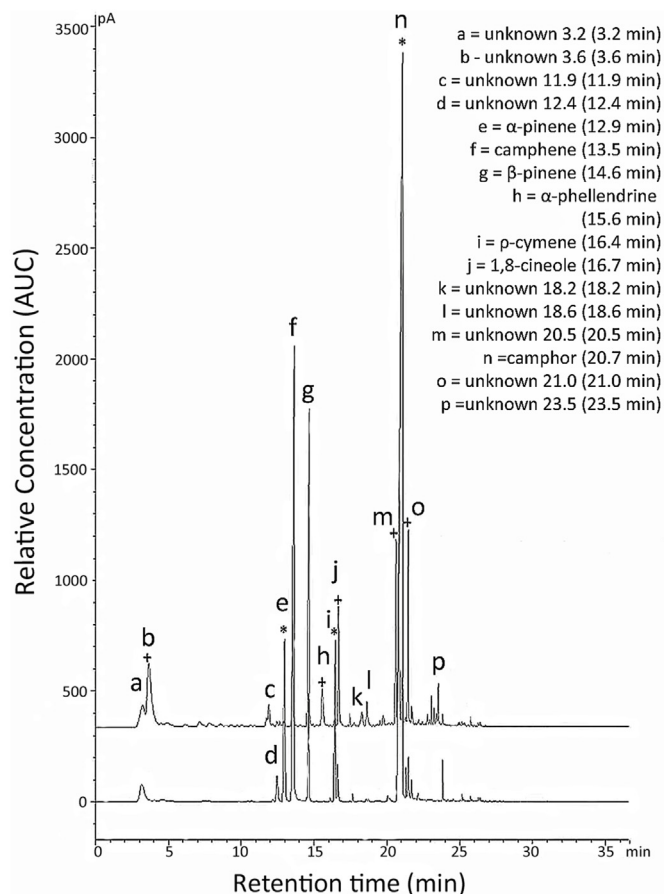


Fig. 2. Representative monoterpene profiles for Wyoming big sagebrush (top line; *Artemisia tridentata wyomingensis*) and three-tip sagebrush (bottom line; *A. tripartita*) from south-central Idaho, USA collected during January 2014. Peaks show individual compounds, with the area under the curve of each peak indicating relative abundance of the compound. Plus signs (+) indicate compounds found only in Wyoming big sagebrush. Compounds are identified using retention time (min) relative to the co-chromatography of known standards.

Table 3

Dominant cover types (Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and three-tip sagebrush (*A. tripartita*) at plots used (Used) by Greater Sage-Grouse (*Centrocercus urophasianus*) and selected at random (Random) during January 2014 in south-central Idaho, USA. Mixed sagebrush cover type included co-dominant Wyoming big sagebrush and three-tip sagebrush.

Cover Type	Used	Random
Wyoming big sagebrush	6	8
Three-tip sagebrush	3	1
Mixed sagebrush	7	7
Total	16	16

phenolics in three-tip sagebrush. Probability of use of a plot declined by a factor of 0.823 for every 1 cm increase in plant height in three-tip sagebrush.

Selection at the plant scale.— For Wyoming big sagebrush, the average concentration of monoterpene Unknown 21.5 was the strongest predictor of diet selection at the plant scale (Table 4, Fig. 5). The probability of use of a plot decreased by a factor of 0.89 for every 1 AUC/100 μ g DW increase in monoterpene Unknown 21.5. For three-tip sagebrush, the best predictor of plant use was crude protein but this parameter had 85% confidence intervals that overlapped 1, indicating this parameter was unreliable for predicting odds of use.

Intensity of use among browsed plants.— Once a plant was selected by

Table 4

Odds ratio estimates and confidence limits (95% and 85%) for top covariates predicting Greater Sage-Grouse (*Centrocercus urophasianus*) use of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) or three-tip sagebrush (*A. tripartita*) in south-central Idaho during January 2014. Analyses were separated by spatial scale, including plot-level and plant-level selection. Covariates with confidence intervals (85% CI) that do not overlap 1.0 are denoted in **bold** and are considered reliable for predicting odds of use. Covariates are ranked in order of increasing AIC_c values for each spatial scale, by species.

Species of sagebrush	Scale	Covariate	Odds ratio	95% CI		85% CI	
				LCL	UCL	LCL	UCL
Wyoming big sagebrush	Plot	Height^a	0.917	−0.145	−0.027	−0.129	−0.043
		Unknown 21.0^b	0.404	−2.069	0.255	−1.760	−0.053
		Unknown 21.5^b	0.887	−0.251	0.013	−0.216	−0.022
Three-tip sagebrush	Plot	Beta-pinene ^b	11.128	−0.304	5.123	0.417	4.402
		Fire history ^c	540	−2868	2880	−2104	2117
		Phenolics^d	1.007	−0.001	0.014	7.979×10^{-4}	0.012
		Height^a	0.823	−0.397	0.007	−0.347	−0.465
	Plant	Crude protein ^e	5.632	−0.421	3.878	0.149	3.307

^a Height (cm).

^b Concentration of monoterpenes in AUC/100 µg dry weight (DW).

^c Fire history measured as years since the most recent fire.

^d Phenolics in µmol of gallic acid equivalents/g DW.

^e Crude protein, % DW.

sage-grouse to be browsed, several factors explained the number of bites on that browsed plant (Table 5). For Wyoming big sagebrush, the number of bite marks per plant was about 2 times higher for plants with higher levels of chemical diversity and there were fewer bite marks for plants with relatively higher concentrations of crude protein and coumarins. For three-tip sagebrush, the best predictor of intensity of use was height above snow. There were about two more bites per plant for every additional centimeter of height of three-tip sagebrush that was above snow (Table 5).

4. Discussion

Overall, biomass of Wyoming big sagebrush was more available to sage-grouse (greater availability across landscape, taller, greater biomass per bite) and provided sage-grouse a higher concentration of crude protein per plant and per bite than three-tip sagebrush. These results suggest that selection of Wyoming big sagebrush for food within this landscape would reduce foraging effort by sage-grouse associated with maximizing intake of crude protein.

However, Wyoming big sagebrush was also more chemically defended than three-tip sagebrush. Wyoming big sagebrush had a greater diversity of individual monoterpenes, the majority of which were in higher concentrations (14 out of 22), with seven monoterpenes not detected in three-tip sagebrush, and higher concentrations of phenolics (Table 1). Unknown 3.2 and 1,8-cineole were in higher concentration in

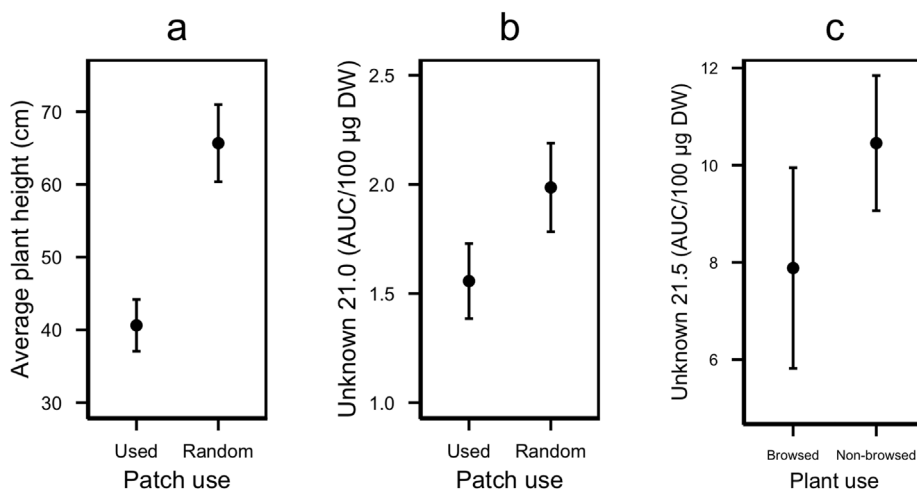


Fig. 3. Plot-scale selection for plant height (cm; a) and concentration of monoterpene Unknown 21.0 (AUC/100 µg dry weight [DW]; b) in Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and plant-scale selection for monoterpene Unknown 21.5 (AUC/100 µg dry weight [DW]; c) in Wyoming big sagebrush by Greater Sage-Grouse (*Centrocercus urophasianus*). Plants were collected in south-central Idaho during January 2014. Graphs show mean $\pm$ SEM.

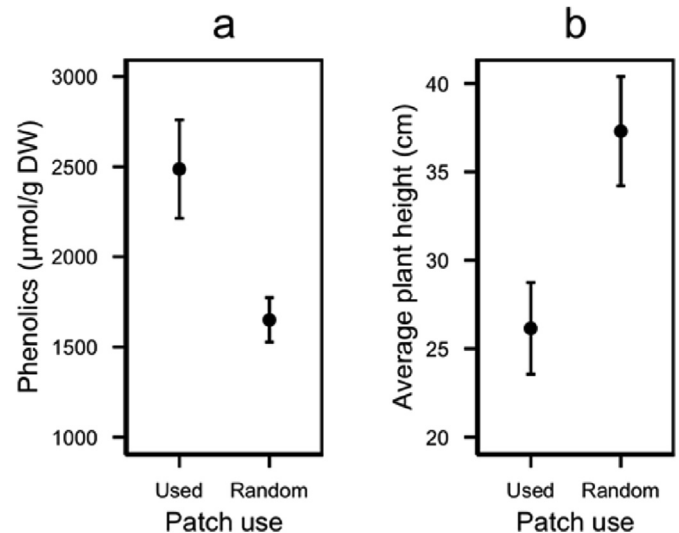


Fig. 4. Plot-scale selection for concentration of phenolics (µmol gallic acid equivalents/g DW; a), and plant height (cm; b) of three-tip sagebrush (*Artemisia tripartita*) by Greater Sage-Grouse (*Centrocercus urophasianus*). Plants were collected in south-central Idaho during January 2014. Graphs show mean $\pm$ SEM.

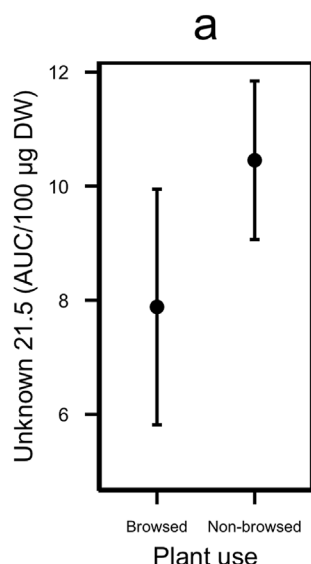


Fig. 5. Plant-scale selection for concentration of unknown monoterpene 21.5 min (AUC/100 µg DW) of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) by Greater Sage-Grouse (*Centrocercus urophasianus*). Plants were collected in south-central Idaho during January 2014. Graphs show mean $\pm$ SEM.

Wyoming big sagebrush and explained avoidance of sagebrush plants and plots, respectively, by sage-grouse in previous studies (Frye et al., 2013). In addition, both 1,8-cineole and camphor (not detected in three-tip sagebrush) inhibited digestive enzymes of sage-grouse (Kohl et al., 2015).

Variation in structural, nutritional, and chemical parameters within and between species of sagebrush is common (Remington and Braun, 1985; Rosentreter, 2004; Kelsey et al., 1982; Frye et al., 2013) and may be explained by both genetic and environmental factors (e.g., Jaeger et al., 2016), such as wildfire. In contrast to previous research suggesting that older burns have higher sagebrush cover and taller plants (Nelle et al., 2000), we found that percent cover and height of both species of sagebrush was similar across burned plots regardless of years since the most recent fire over a 30-year period. One explanation is that the resolution by which fire boundaries are historically mapped is unlikely to detect patches of sagebrush that can survive fire due to fire-breaks associated with roads or rocky terrain (Wambolt et al., 2001; Longland and Bateman, 2002). Based on their trunk diameter the slow recovery of sagebrush is another explanation for the lack of relationship between a relatively short burn history (3–31 years) and the structure of sagebrush. Regardless of time since last fire, the average sagebrush cover ($7.8\% \pm 6.3\%$) at the Bear Trap study area did not meet winter cover guidelines for sage-grouse (Connelly et al., 2000) and was below

the range of percent cover ($15.6 \pm 2.4\%$ to $25.1 \pm 2.2\%$) and height (21.6 ± 4.1 cm to 46.8 ± 4.1 cm) of sagebrush in winter habitats selected by sage-grouse in other areas (Beck et al., 2009; Frye et al., 2013; Holloran et al., 2015). Canopy cover in unburned communities is expected to be between 20 and 35% based on provisional ecological site descriptions of our study area from the Natural Resources Conservation Service. However, relatively low sagebrush cover at our study area is consistent with cover several decades after a burn for other areas that had Wyoming big sagebrush as a dominant or co-dominant species prior to the burn (Beck et al. 2009, 2012; Beck et al. 2009; Beck et al. 2012; Arkle et al., 2014).

The phytochemistry of three-tip sagebrush appeared to be more dependent on fire history than Wyoming big sagebrush with total monoterpenes and one PSMs declining and crude protein, chemical diversity, and percent cover increasing with longer time since last fires. Only one PSM in Wyoming big sagebrush was correlated with the fire history, suggesting that fires may not influence the diet quality of surviving plants of this species to a great extent. This apparent lack of response to fire in Wyoming big sagebrush compared to three-tip sagebrush may be due to the inability of Wyoming big sagebrush to re-sprout, so all new plants would be post-fire seedlings that had not experienced damage during the fire, or where from remaining islands of remnant Wyoming big sagebrush that survived fires without severe damage. In contrast, three-tip sagebrush re-sprouts, and plants may be re-growing and allocating resources towards growth and defense differently than a seedling. Although monitoring of phytochemicals over time within and outside of fire damage is needed to establish causal relationships between fire history and changes in phytochemicals, these results suggest that three-tip sagebrush may have more complex responses to fires than Wyoming big sagebrush. Structurally, Wyoming big sagebrush takes 20–100 years, or more, after fires to recover (Baker et al., 2006; Beck et al. 2009, 2012; Beck et al. 2012) and three-tip sagebrush takes more than fourteen years to recover (Beck et al., 2009). A larger sample size that includes a longer range of fire history and geographical distribution of the two species within and among study areas is needed to disentangle the effects of fire history on phytochemistry and selection of sagebrush by wintering sage-grouse.

Despite differences in availability and diet quality, sage-grouse did not appear to selectively forage on either species at a landscape scale. This apparent lack of species-level selection may reflect two levels of tradeoffs demonstrated in other herbivores: cover versus diet quality (Nersesian et al., 2011; Camp et al., 2013; Crowell et al., 2016; Ulappa et al., 2014) and nutrients versus PSMs (Camp et al., 2013; Bedoya-Pérez et al., 2014). Lack of selection for particular species may be due to overall low shrub availability. Cover within plots at Bear Trap (average $7.8\% \pm 6.3\%$) was lower than shrub cover at other wintering foraging areas for sage-grouse ($17.6\% \pm 4.0\%$, Frye et al., 2013). Despite the relatively low cover at Bear Trap, sage-grouse selected plots with lower cover than random (available) patches. This suggests that dietary

Table 5

Regression lines for top covariates predicting Greater Sage-Grouse (*Centrocercus urophasianus*) intensity of use (number of fresh bite marks per plant) on browsed Wyoming big sagebrush (*Artemisia tridentata wyomingensis*, ATW) or browsed three-tip sagebrush (*A. tripartita*, AT), in south-central Idaho, USA during January 2014. Covariates with confidence intervals (CI) that do not overlap zero are denoted with **bold** text. Covariates are ranked in order of increasing AIC_c values, by species.

Species of Sagebrush	Covariate	Intercept	Slope	95% CI		85% CI	
				LCL	UCL	LCL	UCL
Wyoming big sagebrush	Chemical diversity^a	−11.36	27.91	1.774	54.048	9.267	46.556
	Crude protein^b	121.91	−5.83	−11.954	−0.300	−10.197	−1.456
	Coumarins ^c	46.53	−1.18	−2.640	0.276	−2.222	−0.142
Three-tip sagebrush	Height above snow^d	−14.51	2.18	0.484	3.885	1.022	3.347

^a Monoterpene diversity calculated as a Shannon Index, incorporating evenness and abundance of major compounds.

^b Crude protein, % DW.

^c Total coumarins in µmol of scopoletin equivalents/g DW.

^d Height of plant (cm) minus height of snow (cm), when snow was present; otherwise measured as height of plant.

quality or other structural features may be driving selection more than cover at this study area. The study area's extensive fire history (31/32 plots burned in the 31 years preceding the study) may have reduced habitat quality to the point that this area does not allow sage-grouse to select structural resources similar to what has been observed in areas not affected by fire (Remington and Braun, 1985; Frye et al., 2013). As a result, sage-grouse in this study may be using habitats that do not fall within recommended guidelines (Connelly et al., 2000b) and have structural features that may compromise population stability (Foster et al., 2018; Smith and Beck, 2018).

Our data suggest that a trade-off between shrub height and diet quality may explain the lack of selection for species by sage-grouse. Shrub height is important to herbivores because moderately sized plants allow herbivores to see approaching predators, while remaining relatively concealed (Camp et al., 2013). Although three-tip sagebrush was less available (30% of shrubs at random plots, 35% of shrubs at used plots) than Wyoming big sagebrush (70% of shrubs at random plots, 65% of shrubs at used plots), had lower biomass per bite, and had less crude protein, it was within the recommended shrub height. In contrast, Wyoming big sagebrush was taller than recommended in habitat guidelines (Connelly et al., 2000b), and had a greater mean height above snow compared to other research on winter habitat use by sage-grouse in areas dominated by big sagebrush species (19.9–35.6 cm above snow, Beck, 1977; 28.8–43.3 cm above snow, Hupp and Braun, 1989; 46.8 ± 4.1 cm, Beck et al., 2009; 21.6 ± 4.1 cm, Holloran et al., 2015). Selection for generally shorter plants, such as dwarf sagebrush species, as a forage resource has been documented in winter habitat where the taller plants were primarily Wyoming big sagebrush with higher PSMs (Frye et al., 2013). Use of three-tip sagebrush by sage-grouse could therefore be due to selection for a more optimal height despite lower biomass and nutrient quality compared to Wyoming big sagebrush. In other research, snow cover impacted winter habitat use for sage-grouse, with grouse selecting foraging areas with lower snow cover and depth like south-facing slopes (Beck, 1977; Carpenter et al., 2010), but the low snowpack did not appear to impact habitat use. This study was conducted with relatively low snow pack (average = 6 cm), and therefore results cannot be extrapolated to other study sites or years with high snow cover, as three-tip sagebrush may not be as available as taller Wyoming big sagebrush plants given its relatively lower height. Availability of shorter sagebrush plants may become more limited during high snow years, which may affect selection at a species level.

Lack of selection for particular species may also be due to trade-offs among phytochemicals. There is extensive documentation that herbivores select plants with relatively higher protein and lower PSM concentrations (Thacker et al., 2012; Frye et al., 2013; Ulappa et al., 2014; Wing and Messmer, 2016). No one species of sagebrush at our study area offered both higher protein and lower PSMs. While Wyoming big sagebrush had higher crude protein, it also had higher phenolics, a greater diversity of monoterpenes, and higher concentrations of 12 individual monoterpenes and several potentially unique monoterpenes (Table 1) compared to three-tip sagebrush. The benefit of higher protein content in Wyoming big sagebrush may be offset by some of the unique chemicals or higher concentrations of particular monoterpenes that may inhibit protein digestion (e.g., 1,8-cineole, Kohl et al., 2015). The potential toxicity of Wyoming big sagebrush could be diluted by consuming three-tip sagebrush, which has lower concentrations of these individual monoterpenes. However, three-tip sagebrush had a higher overall concentration of monoterpenes driven by two individual monoterpenes (Unknown 21.0 and Unknown 21.5) that were higher than any single monoterpene in Wyoming big sagebrush (Table 1). It is possible that consuming both species of sagebrush allows sage-grouse to diversify the PSMs consumed and minimize overloading any one detoxification pathway (Marsh et al., 2006). The mechanism of action and effective concentration of single chemicals or mixture is needed to understand why certain species of sagebrush are selected by sage-

grouse or not.

Although sage-grouse did not select species of sagebrush based on known structural or dietary differences, these plant characteristics influenced selection at plot and plant scales within species. At the plot-scale, used plots of Wyoming big sagebrush had lower concentrations of monoterpene Unknown 21.0, and at the plant scale selected plants had lower concentrations of monoterpene Unknown 21.5. This selection within a species supported our hypothesis that sage-grouse may select dietary resources with lower concentrations of PSMs. For both species of sagebrush, selection matched previous literature, with sage-grouse selecting plants of moderate height and plants with lower PSMs (monoterpenes Unknown 21.0 and Unknown 21.5; Remington and Braun, 1985; Thacker et al., 2012; Frye et al., 2013; Wing and Messmer, 2016).

Given the expected expansion of three-tip sagebrush (Baker, 2006; Dalgleish et al., 2011) and potential range contractions for other species of sagebrush (Shafer et al., 2001), three-tip sagebrush may become an increasingly important species for wildlife as both cover and forage. Although Lowe et al. (2009) found that sage-grouse hens did not select three-tip sagebrush for nest cover more than expected based on availability, our study found that three-tip sagebrush is eaten by sage-grouse during winter. Results also demonstrate that selection of sage-grouse is spatially and temporally dependent. Wyoming big sagebrush avoided by sage-grouse at one study area (Frye et al., 2013), may not be avoided at another study area (this study), and three-tip sagebrush avoided during nesting (Lowe et al., 2009), may not be avoided during winter foraging (this study). Given the diverse uses of sagebrush over space and time, management practices that maintain structural and chemical diversity may have the greatest benefit to sage-grouse and other wildlife.

5. Management implications

This is the first formal documentation of sage-grouse eating three-tip sagebrush as well as the first account describing the chemistry (besides protein, Fraker-Marble et al., 2007) of three-tip sagebrush. Our study suggests that three-tip sagebrush in post-fire environments may provide acceptable alternative forage while big sagebrush taxa re-establish. However, sage-grouse do consume sub-optimal food resources as other more palatable species are depleted (Welch et al., 1991). Therefore, use of food resources or habitats within one study area does not indicate that the individuals using those resources will have the same fitness as individuals using optimal resources. Given the varying structural and phytochemical characteristics of sagebrush species and the dynamic responses of PSMs after fire, it is unlikely that any single species or subspecies of sagebrush can meet the habitat requirements for sage-grouse across their life history. We suggest that managers should attempt to maintain or, after fire, restore a diversity of locally adapted sagebrush species present within an ecological site to provide diverse dietary and structural resources for wildlife. Additional monitoring of changes in food composition, biomass availability, and quality are needed to understand, predict, and manage how fire or other outcomes of climate changes influence the demographics of sage-grouse and other herbivores. Post-fire restoration efforts require monitoring that measure success first by the re-establishment of pre-disturbance sagebrush species offering a diversity of functional cover and food, and second by the population response of sage-grouse and other species of interest to those restoration efforts.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2020.104154>.

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