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Terry A. Messmer, *Utah State University*

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Impact of sagebrush nutrients and monoterpenes on greater sage-grouse vital rates

Brian R. Wing, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA

Terry A. Messmer, Jack H. Berryman Institute, Department of Wildland Resources, Utah State University, Logan, UT 84322-5230, USA *terry.messmer@usu.edu*

Abstract: Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) depend on sagebrush (*Artemisia* spp.) to complete its annual life cycle. The winter diet for sage-grouse consists almost entirely of sagebrush leaves, and individual birds may gain weight while foraging on sagebrush. Previous studies have reported higher crude protein and lower monoterpene concentrations in the sagebrush species selected as winter forage by sage-grouse. However, no studies have attempted to link female sage-grouse vital rates (i.e., nest initiation and success, egg fertility, clutch size, and adult survival) to crude protein or monoterpene concentrations of sagebrush plants browsed during pre-nesting periods. From March to May 2013, we monitored pre-nesting diets for 29 radio-marked female sage-grouse in the Box Elder Sage-grouse Management Area in northwestern Utah to determine if a relationship existed between foraging patterns and vital rates. We randomly located radio-marked female sage-grouse ≥3 times during the study period and subsequently sampled 70 sagebrush communities where they were observed to determine which sagebrush species or subspecies were browsed and if samples collected of the browsed plants differed in nutritional quality (i.e., crude protein) and chemical composition (i.e., monoterpenes) from non-browsed plants in the areas sampled and non-browsed randomly selected plants in adjacent sagebrush communities. Seventy-three percent of these sites where radio-marked females were located consisted entirely of black sagebrush (*A. nova*) communities. Percent crude protein and total monoterpene concentration in black sagebrush and Wyoming big sagebrush (*A. tridentata wyomingensis*) did not differ between browsed, non-browsed, and non-browsed random plants. Browsed black sagebrush plants were lower in average percent crude protein (P = 0.003) and higher in total monoterpene concentration ($P \leq 0.001$) than browsed Wyoming big sagebrush. Apparent nest success, age of nesting females, egg fertility, clutch size ($P > 0.05$), and female monthly survival rates (CI = -0.21–0.49) for the radio-marked sage-grouse we monitored did not differ based on sagebrush crude protein and total monoterpene content. However, all of the radio-marked female sage-grouse (n = 10) observed in black sagebrush communities where the collected plant samples exhibited higher concentrations of an unidentified monoterpene successfully hatched nests (P = 0.002). All of the nests of radio-marked female sage-grouse (n = 9) outside these areas failed. Our results lend additional support to previous published work regarding sage-grouse preferences for black sagebrush as pre-nesting forage and suggest a potential link to nest success.

Key words: *Artemisia* spp., *Centrocercus urophasianus*, diet, greater sage-grouse, monoterpene, nest success, pre-nesting forage, sagebrush

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) depend on sagebrush (*Artemisia* spp.) as both a primary forage and preferred cover (Connelly et al. 2011). The winter diet of sage-grouse consists almost entirely of sagebrush leaves (Patterson 1952, Dalke et al. 1963). Despite the defensive chemistry of sagebrush (Striby et al. 1987, Rosentreter 2005), sage-grouse are well adapted to a sagebrush diet and may even gain weight when foraging on the plant during the winter months (Beck and Braun 1978).

Plant secondary metabolites (PSMs), such as monoterpenes, sesquiterpene lactones, and phenolics, are typically considered to be a toxic defense of plants that are often avoided by herbivores (Forbey et al. 2013*a*). Sagebrush is relatively high in PSMs (Kelsey et al. 1982), and the effect of these chemical compounds on sage-grouse digestion or productivity is not fully understood (Forbey et al. 2013*b*). Published information on the palatability of sagebrush is incomplete and consists mostly of observations on other wildlife species (Rosentreter 2005, Fryer 2009).

Frye et al. (2013) reported that sage-grouse in south-central Idaho preferred black sagebrush (*A. nova*) to Wyoming big sagebrush (*A. tridentata wyomingensis*), despite the higher level of crude

protein found in the latter. Presumably, black sagebrush was selected because of its lower concentration of PSMs. Remington and Braun (1985) reported a similar relationship in Colorado, where Wyoming big sagebrush was preferred over mountain big sagebrush (*A. t. vaseyana*), apparently due to higher protein and lower monoterpene content. Remington and Braun (1985) and Frye et al. (2013) also reported higher levels of crude protein in browsed plants than non-browsed and random plants, but differences of monoterpene concentrations in browsed plants were reported only by Frye et al. (2013). Neither of these studies attempted to differentiate forage selection patterns by sex or age, or the effects of these selection patterns on population vital rates by sagebrush type.

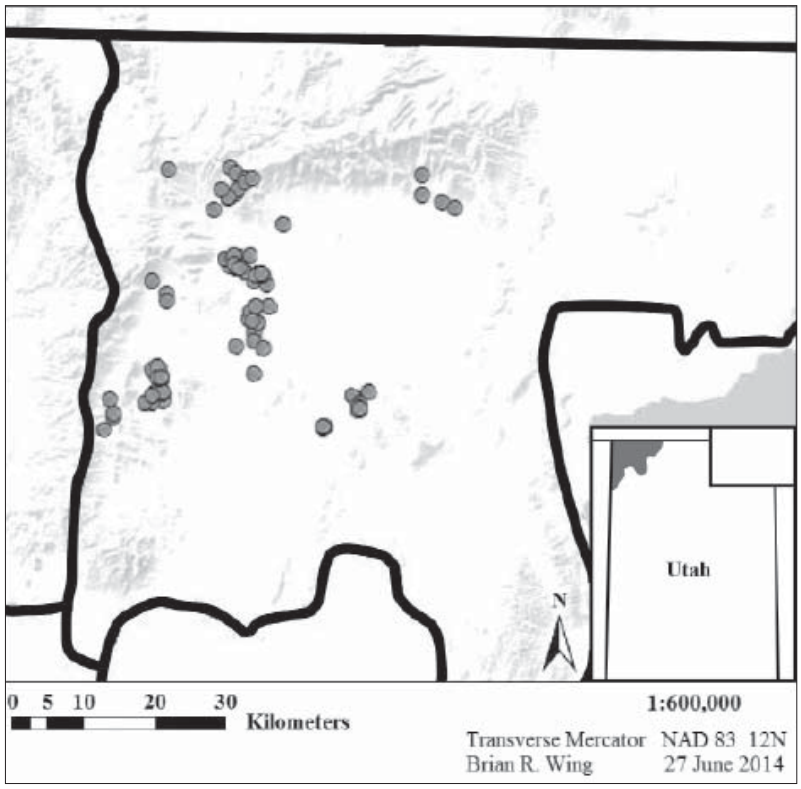


Figure 1. Documented sagebrush (*Artemisia* spp.) browse sites of female greater sage-grouse (*Centrocercus urophasianus*) in Box Elder Sage-Grouse Management Area in northwestern Utah, March to April 2013.

Two types of black sagebrush exist in western North America. "Type A" is considered highly palatable, while "type B" is low in palatability (Rosentreter 2005). Wyoming big sagebrush plants also may hybridize with mountain big sagebrush (McArthur et al. 1988, Freeman et al. 1991).

Thacker et al. (2012) suggested that the nutritional quality and chemical composition of the sagebrush plants selected as forage by sage-grouse may affect overall bird fitness. It is possible that the diet of a female sage-grouse could even affect egg production (e.g., clutch size, egg fertility, and hatching success), as some studies involving other bird species have demonstrated (Bauer 1985, Eldridge and Krapu 1988). If adult survival or female reproductive rates differ among individual sage-grouse based on crude protein or monoterpene level in the plants they select for forage, managers also may need to consider the availability and species composition of sagebrush communities when developing conservation plans. This information may be particularly important if climate change causes an increase in plant chemical defenses and thus affects the availability and palatability of sagebrush (Forbey et al. 2013*b*). To our knowledge, no research has been published describing a potential link between female sage-grouse pre-nesting sagebrush diet selection patterns and vital rates.

The purpose of our research was to describe female sage-grouse sagebrush foraging patterns during the pre-nesting season. Specifically, we wanted to determine if individual sagebrush plants browsed by sage-grouse during this period differed from non-browsed and non-browsed random plants in their nutritional quality and chemical composition. Lastly, we were interested in determining if the phytochemistry of browsed plants affected individual female sage-grouse nest initiation and success, egg fertility, and clutch size, and adult survival rates.

Study area

Our research was conducted within Utah's Box Elder Sage-Grouse Management

Area (SGMA; Utah Division of Wildlife Resources [UDWR] 2009, 2013). The study area encompasses approximately 440,750 ha in the northwest corner of Utah in Box Elder County (Figure 1). Land ownership is a mosaic of federal, state, and private lands. Common land uses included grazing by domestic livestock, hay production, and rock quarrying. Within the SGMA, we concentrated our efforts on winter habitats, which encompassed approximately 39,540 ha and ranged from 1,500–2,500 m above sea level in elevation.

The most common sagebrush species in the study area were Wyoming, basin (*A. t. tridentata*), black, and mountain big sagebrush subspecies. Other sagebrush species present included low (*A. arbuscula*), bud (*A. spinescens*), and pygmy (*A. pygmaea*). Proportions of sagebrush cover in the primary study area were approximately 55% Wyoming and basin big sagebrush, 34% black sagebrush, and 11% mountain big sagebrush (U.S. Geological Survey [USGS] 2004).

Other shrub and tree species present included rabbitbrush (*Chrysothamnus* spp.), greasewood (*Sarcobatus vermiculatus*), horsebrush (*Tetradymia* spp.), antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier utahensis*), snowberry (*Symphoricarpos* spp.), juniper (*Juniperus* spp.), and pinyon pine (*Pinus* spp.). Common forb species included milkvetch (*Astragalus* spp.), phlox (*Phlox* spp.), hawksbeard (*Crepis* spp.), western yarrow (*Achillea millefolium*), and lupine (*Lupinus* spp.). Native and introduced grasses included Indian ricegrass (*Achnatherum hymenoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), bluegrasses (*Poa* spp.), Great Basin wildrye (*Elymus cinereus*), crested wheat (*Agropyron cristatum*), and cheatgrass (*Bromus tectorum*).

The climate of the study area is typical of the Great Basin with cold winters and hot summers (West 1983). Average temperatures ranged from a low of -10°C in January to a high of 29°C in July. Average annual precipitation is 34 cm. Average annual snowfall is 92 cm (Western Regional Climate Center 2014). In 2013, winter temperatures were often below -20°C, the snow level persisted in the valley, and spring precipitation was greater than in 2012.

Methods

Sage-grouse monitoring

We captured and radio-marked female sage-grouse from January 2012 to April 2013 following protocols described by Connelly et al. (2003). Birds were captured at night in 2-person teams using an all-terrain vehicle, spotlight, and long-handled net. Each captured bird was fitted with a numbered leg band and a 20-g necklace-type Advanced Telemetry Systems™ (ATS; Advanced Telemetry Systems, Insanti, MN, USA) radio transmitter (150.000–151.000 MHz) equipped with a mortality sensor. Captured birds were sexed, aged (Eng 1955), and weighed using a PesolaTM (Pesola, Baar, Switzerland) 2,500-g spring scale. We recorded the capture location using a handheld global positioning system (GPS) unit (UTM, 12N, NAD 83). We handled the radio-marked birds with care and they were released on site according to protocol approved by the Utah State University Institutional Animal Care and Use Committee (IACUC #1194) and UDWR Certificate of Registration (COR #2BAND8743).

We monitored the radio-marked sage-grouse to determine vital rates and habitat use patterns using Communications SpecialistsTM (Communications Specialists, Orange, CA, USA) and Telonics™ (Telonics, Mesa, AZ, USA) receivers, handheld 3-element Yagi antennas, and vehicle-mounted omni-directional antennas. We used a small fixed-wing aircraft fitted with ATSTM radio telemetry equipment to locate birds we could not detect through ground radio telemetry. We used a handheld GPS unit to mark the geographic location each time a radio-marked bird was relocated. Radio-marked females were located at least weekly during the breeding season and twice each week during the nesting period. We also located radio-marked birds as soon as possible when a transmitter emitted a mortality signal.

We determined that radio-marked female sage-grouse were nesting when the bird was recorded in the same location on 2 consecutive visits during the breeding season. Nesting females were located using handheld telemetry equipment and binoculars. To mitigate nest abandonment, we exercised caution to not disturb the nesting females. We marked nest locations by GPS and inconspicuous physical markers, which consisted of small rock piles



Figure 2. Mountain big sagebrush (*Artemisia tridentata vaseyana*) leaves collected in northwestern Utah, spring 2013, showing the typical appearance of leaves browsed by greater sage-grouse (*Centrocercus urophasianus*).

located ≥30 m at random cardinal directions from the nest. Nesting females were carefully observed 2–3 times each week until the nest hatched or failed. A successful hatch was determined when egg halves were found intact in or near the nest bowl or the inner membrane of the egg was separated from the shell (Klebenow 1969, Wallestad and Pyrah 1974).

In March and April 2013, we visually located wintering sage-grouse flocks by tracking radio-marked females. Because of snow depths, we were limited to locations that were readily accessible on foot. From this sample, we randomly selected radio-marked sage-grouse for subsequent observation.

Once a sage-grouse flock containing a radio-marked female was located, we searched the sagebrush patch for sagebrush plants that had been freshly browsed by sage-grouse. We determined which plants had been browsed by examining leaves for evidence of a typical cut leaf pattern of sage-grouse foraging (Remington and Braun 1985; Figure 2). When we determined that a patch had been browsed by the sage-grouse flock, the browsed sagebrush was identified to subspecies. We obtained ≥3 locations, on different days, for multiple radio-marked female sage-grouse in their associated flocks.

We collected leaf tissue samples from browsed, non-browsed, and non-browsed random sagebrush plants at locations where radio-marked females were observed. We analyzed these samples to determine if the browsed and non-browsed plants differed based on nutritional quality and chemical composition. Non-browsed plants within each foraging site were selected by finding the nearest plant of the same subspecies that showed no signs of sage-grouse foraging. Non-browsed random plants of the same subspecies were selected in a random direction and distance between 300 m and 1 km of the browse site. We identified each

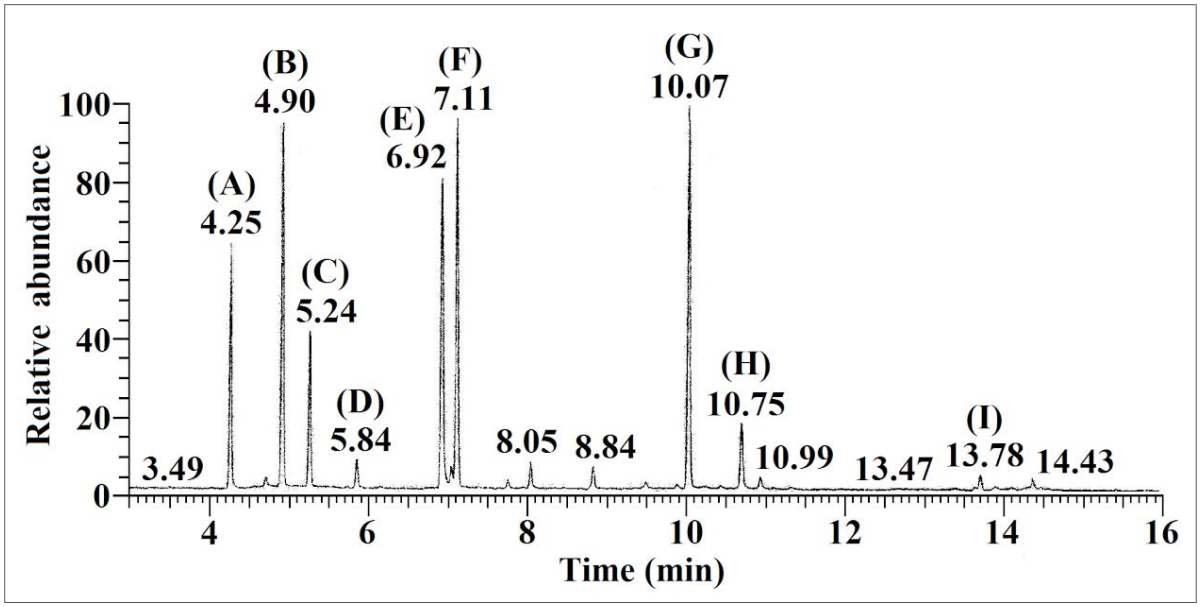


Figure 3. Typical monoterpene profile of black sagebrush (*Artemisia nova*) sampled in northwestern Utah, March to April 2013, produced by gas chromatography (primary peaks are labeled A–I).

sagebrush plant to subspecies and sampled by collecting enough live and leafy stems to fill a 0.2-L NascoTM (Nasco, Fort Atkinson, WI, USA) Whirl-Pak® bag. Plant tissue samples were stored frozen at -10°C until they were tested.

Nutrient analysis

Analyses of the nutritional quality and chemical composition of the collected sagebrush samples were performed at the U. S. Department of Agriculture (USDA) Poisonous Plants Research Lab in Logan, Utah. To determine nutritional quality, sagebrush leaves were oven dried at 40°C and ground using a mortar and pestle. Each dried sample was analyzed using a Leco Corp.TM (Leco Corporation, St. Joseph, MI, USA) FP-528 testing instrument to determine the percentage of crude nitrogen. The percentage of crude protein on a partial-dry sample was calculated by multiplying the percentage of crude nitrogen by 6.25 and 100, then dividing by the percentage of dry matter. Each sample was analyzed twice and the resulting percentages were averaged.

To analyze the chemical composition of the sagebrush samples, 100 mg of non-dried and non-ground sagebrush leaves were weighed and placed in a 10-mL screw-cap test tube. We used glass pipettes and battery-operated pipettor to add 5 mL of 0.186 mg/mL octaphenone methylene chloride solvent to each test tube. The tubes were capped tightly and allowed to sit for 24 hours. Samples were then filtered through a glass pipette containing paper and sodium sulfate and transferred to a 1.5-mL test vial and tightly capped. Samples were then analyzed for monoterpene concentration using a Thermo FinniganTM (Thermo Finnigan LLC, San Jose, CA, USA) Polaris Trace gas chromatography mass spectrometer testing instrument. Samples were analyzed in groups of approximately 30 samples during each testing period. The analysis was repeated for 1 sample up to 4 times to determine accuracy and consistency between testing periods. The accuracy and consistency of the testing process was further validated by inspecting the profiles of each sample for the typical monoterpene peaks of black or Wyoming big sagebrush (Thacker et al. 2012). The analysis was also verified by plotting the concentration of primary monoterpenes against the total monoterpene concentration to check for a linear regression pattern.

Data analysis

We analyzed the selection patterns for sagebrush species for radio-marked female sage-grouse observed at ≥3 browse sites. We calculated the percentages of the radio-marked sage-grouse, by sex and age, which were observed in browsed patches of black sagebrush, big sagebrush, or

both sagebrush species. We used an occupancy estimation model in Program MARK software (MARK Version 7.1, http://warnercnr.colostate.edu/~gwhite/mark/mark.htm, accessed August 27, 2013) to calculate probabilities for observed radio-marked female sage-grouse, by sex and age, using browsed patches of black sagebrush over browsed patches of big sagebrush in their first 3 encounters.

We calculated nest initiation percentages as the proportion of radio-marked female sage-grouse alive at the onset of the nesting period that nested. Re-nesting effort was calculated as the proportion of females that survived the failure of an initial nest and made a second attempt to nest. Apparent nest success was calculated as the proportion of nests with ≥1 hatched egg. Hatching success was calculated as the proportion of all eggs that hatched in successful nests. Clutch size was the total number of eggs laid. Egg fertility was calculated as the proportion of eggs laid in a nest that had either hatched or contained a partially developed embryo. Depredated nests were not included in the egg fertility or clutch size calculations because egg shells were often missing or crushed.

Statistical analyses of sagebrush nutrition and chemical content and associated vital rate data consisted of descriptive statistics, paired 2-tailed *t*-tests, and a linear regression model, each performed in R statistical software (R Version 2.15.1, http://www.r-project.org, accessed March 8, 2013). We used *t*-tests to determine if female sage-grouse age, capture weight (excluding birds captured during or prior to the 2012 breeding season), nest initiation, and apparent nest success differed relative to crude protein and monoterpene concentrations of browsed, non-browsed, and non-browsed random sites associated with individual radio-marked female sage-grouse. We used a linear regression model to analyze the effects of sagebrush nutritional and chemical content on clutch size, egg fertility, and hatching success. All results were considered significant at $P < 0.05$.

We used a known-fate analysis with logit link function in Program MARK to calculate monthly survival probabilities of female sage-grouse from March to May 2013. We included the percentage of crude protein and total monoterpene concentration of black sagebrush collected at browse sites associated with individual radio-marked females as covariates in this analysis to determine if they were related to female monthly survival rates during the breeding season. All sage-grouse included in the survival analysis had survived ≥1 week after capture to ensure that mortalities were not related to capture trauma. We used a 95% confidence interval (CI) to determine the significance of covariate effects. A confidence interval including 0 indicated that an effect was not significant.

Results

From March 1 to April 19, 2013, we identified 70 sites throughout our study area where radio-marked females were observed in sage-grouse flocks. Flocks ranged in size from 2–40 birds and usually flushed 100 m from the approaching researcher. This made observations of direct browsing behavior of individual radio-marked female sage-grouse difficult. Flocks were typically segregated by sex but sometimes consisted of both females and males. We recorded flocks in sagebrush patches consisting of black sagebrush, Wyoming big sagebrush, and mountain big sagebrush. We detected 18 radio-marked female sage-grouse (8 adults and 10 yearlings) at ≥3 flock sites. Fifty-one (73%) female flock sites occurred in black sagebrush. We did not observe any radio-marked adult females at flock sites consisting of only Wyoming big sagebrush. However, 3 radio-marked adults were observed at flock sites consisting of both sagebrush species. We observed 1 radio-marked juvenile female using only black sagebrush foraging sites and 4 using sites consisting of both sagebrush species. Probabilities that the radio-marked sage-grouse used patches of black sagebrush over big sagebrush were 0.95 (SE = 0.05) for females combined, 0.77 (SE = 0.10) for adults, and 0.91 (SE = 0.09) for yearlings.

From the 70 flock sites, we were able to identify and collect browsed sagebrush leaf tissue samples from 36. These samples were used to conduct the nutritional analysis. Twenty-four sites were located in black sagebrush and 12 in Wyoming big sagebrush. The black sagebrush type we analyzed was "type A." The Wyoming sagebrush we analyzed was classified as a hybrid of Wyoming and

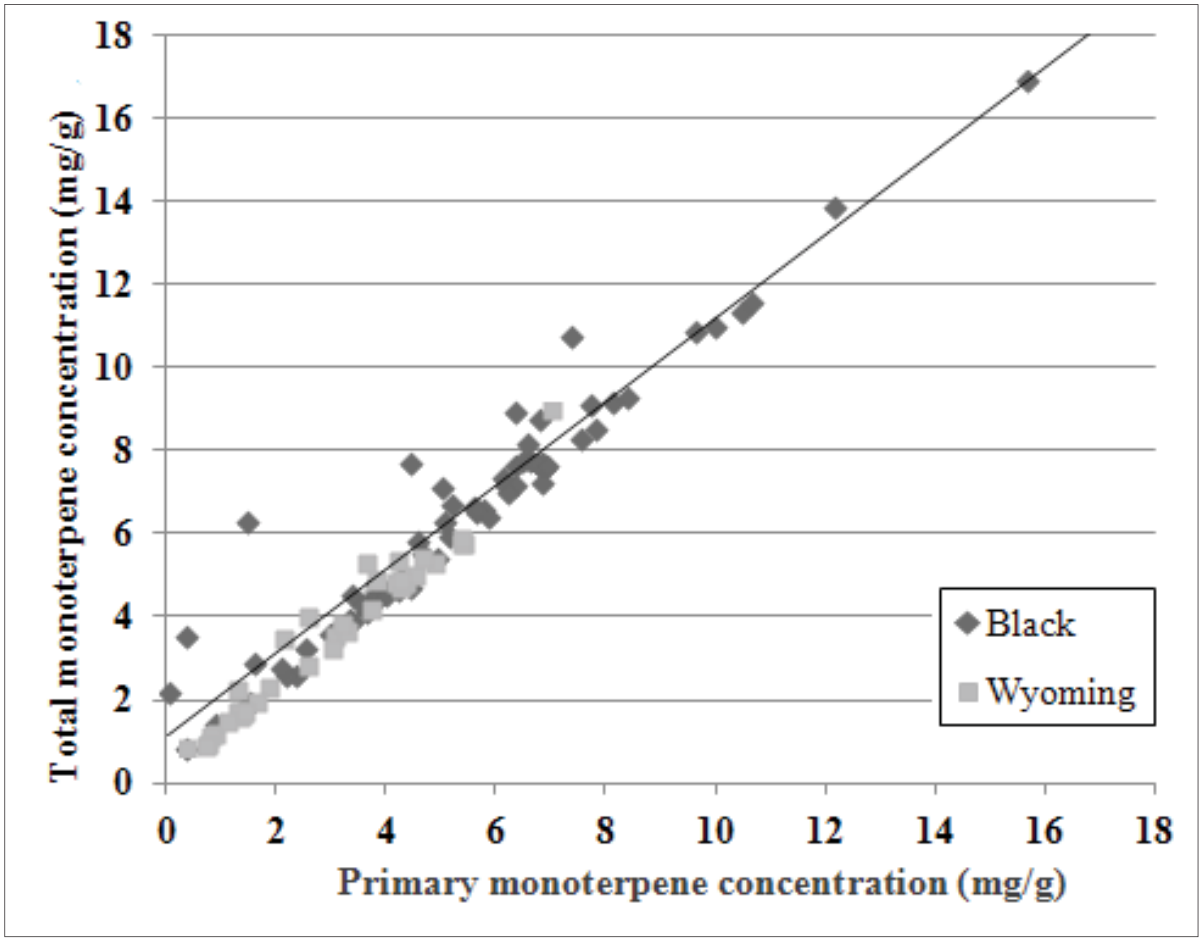


Figure 4. Primary versus total monoterpene concentration in black sagebrush (*Artemisia nova*) and Wyoming big sagebrush (*A. tridentata wyomingensis*) sampled at browsed, non-browsed, and non-browsed random sites in northwestern Utah, March to April 2013.

mountain big sagebrush because it emitted a moderate fluorescence under a UV-light test (Rosentreter 2005).

For both black sagebrush and Wyoming big sagebrush, the crude protein content varied 0.1–3.0% ($\bar{x}$ = 0.66, SE = 0.08) between the first and second analyses. The average percentage of crude protein did not differ between browsed and non-browsed sites (t = 0.04, df = 46, P = 0.97; t = 0.39, df = 17, P = 0.7), browsed and non-browsed random sites (t = 0.35, df = 46, P = 0.73; t = 0.69, df = 22, P = 0.50), and non-browsed and non-browsed random sites (t = 0.39, df = 46, P = 0.7; t = 0.85, df = 18, P = 0.41) for black sagebrush and Wyoming big sagebrush, respectively.

The average percentage of crude protein was greater in Wyoming big sagebrush than black sagebrush at browsed (t = 3.37, df = 21, P = 0.003), non-browsed (t = 2.4, df = 14, P = 0.03), and non-browsed random sites (t = 2.46, df = 18, P = 0.03). Crude protein in black sagebrush samples averaged 16.8% (SE = 0.36, range = 12.9–20.2) at browsed sites, 16.8% (SE = 0.36, range = 12.8–20.4) at non-browsed sites, and 16.6% (SE = 0.3, range = 13.6–20.9) at non-browsed random sites. Crude protein in Wyoming big sagebrush samples averaged 18.9% (SE = 0.55, range = 17.1–23.5) at browsed sites, 19.4% (SE = 0.6, range = 15.8–27.5) at non-browsed sites, and 18.4% (SE = 1.0, range = 15.6–22.0) at non-browsed random sites. We did not observe a difference between black sagebrush and Wyoming big sagebrush in elevation of browse sites (t = 0.55, df = 30, P = 0.64).

To calibrate the monoterpene lab analysis of black sagebrush, 1 sample was analyzed 4 times with a day between each analysis. The total concentration of monoterpenes in the sample differed 1.0 mg/g (SE = 0.2) between the first and fourth analyses, which was determined to be an acceptable amount of variation (D. Gardner, USDA Poisonous Plants Research

Lab, personal communication). Sixty-nine of the 72 samples consistently matched the typical black sagebrush profile (Figure 3). The samples with inconsistent profiles were also apparent in the plot of primary and total monoterpene concentration, but overall, the sample points consistently followed a linear regression line (Figure 4). The total monoterpene concentration of the inconsistent samples was within range of the other samples, so we included them in the statistical analyses. Nine primary unidentified monoterpenes (labeled A–I) were determined to exist in the typical profile of the black sagebrush samples.

The monoterpene analysis of Wyoming big sagebrush samples was conducted 2 months after the black sagebrush analysis. Ten of the previously tested black sagebrush samples were re-extracted and included as a control group in this analysis to confirm consistency between the 2 analyses. The black sagebrush samples differed an average of 1.0 mg/g (SE = 0.2) from the first testing period, which, considering these samples were re-extracted, was determined acceptable for comparisons between the 2 testing periods (D. Gardner, USDA Poisonous Plants Research Lab, personal communication). One Wyoming big sagebrush sample was analyzed 3 times and differed 0.1 mg/g (SE = 0.03). Twenty-six (72%) of the Wyoming big sagebrush samples were consistent in profile, while the remaining 10 samples exhibited a similar profile but with 1 particular monoterpene in much greater concentration. Overall, the Wyoming big sagebrush samples varied more than the black sagebrush in presence of individual monoterpenes, ranging from 6–15 primary ($\bar{x}$ = 11.6, SE = 0.3) unidentified monoterpenes.

Total monoterpene concentrations did not differ between browsed and non-browsed sites (t = 0.1, df = 44, P = 0.93; t = 0.2, df = 20, P = 0.85), browsed and non-browsed random sites (t = 0.1, df = 46, P = 0.96; t = 0.5, df = 22, P = 0.66), and non-browsed and non-browsed random sites (t = 0.1, df = 44, P = 0.98; t = 0.2, df = 20, P = 0.85) within black sagebrush and Wyoming big sagebrush, respectively. Total monoterpene concentration was greater in black sagebrush than Wyoming big sagebrush at browsed (t = 3.9, df = 34, $P \leq$ 0.001), non-browsed (t = 3.52, df = 24, $P \leq$ 0.001), and non-browsed random sites (t = 3.4, df = 34, $P \leq$ 0.001). We also analyzed the concentration levels of primary monoterpenes in both species, and these did not differ between browsed, non-browsed, and non-browsed random sites ($P >$ 0.05). Total monoterpene concentration of black sagebrush averaged 6.3 mg/g (SE = 0.6, range = 1.4–11.6) at browsed sites, 6.4 mg/g (SE = 0.5, range = 1.9–13.9) at non-browsed sites, and 6.4 mg/g (SE = 0.3, range = 0.9–16.9) at non-browsed random sites. Total monoterpene concentration of Wyoming big sagebrush averaged 3.3 mg/g (SE = 0.4, range = 0.9–5.8) at browsed sites, 3.6 mg/g (SE = 0.7, range = 0.9–5.4) at non-browsed sites, and 3.4 mg/g (SE = 0.5, range = 0.8–8.9) at non-browsed random sites.

Black sagebrush and sage-grouse vital rates

Non-browsed and non-browsed random sagebrush samples were also analyzed in association with each browse site. Because the radio-marked female sage-grouse exhibited a higher probability of use for black sagebrush, we were unable to obtain a sufficient number of Wyoming big sagebrush samples for our vital rate analysis. Thus, our analyses of the effects of sagebrush nutrition and chemical composition on vital rates included only black sagebrush samples.

Black sagebrush samples associated with individual nesting females did not differ by female age (t = 0.9, df = 17, P = 0.38), nest initiation (t = 0.3, df = 8, P = 0.76), nest success (t = 0.1, df = 17, P = 0.99; t = 0.7, df = 16, P = 0.53), clutch size (P = 0.91; P = 0.51), hatching success and egg fertility for percent crude protein (P = 0.57) and total monoterpene concentration (P = 0.44; Table 1). We did not observe a difference in capture weight (excluding captures from the previous year) between the associated nesting females by age (t = 0.2, df = 7, P = 0.99) or nest success (t = 0.8, df = 4, P = 0.29).

The unidentified monoterpene, labeled as "B," was more concentrated in black sagebrush samples from browse sites associated with successful nesting females ($\bar{x}$ = 1.2 mg/g, SE = 0.1) than sites used by unsuccessful females ($\bar{x}$ = 0.6 mg/g, SE = 0.1; t = 3.0, df = 17, P = 0.01). Overall, monoterpene B was the second most concentrated of the 9 primary monoterpenes, averaging 0.8 mg/g (SE = 0.1). There were no differences in primary monoterpene

Table 1. Greater sage-grouse (*Centrocercus urophasianus*) female nest initiation and apparent nest success relative to the nutritional and chemical content of black sagebrush (*Artemisia nova*) samples collected at browse sites in northwestern Utah, March to April 2013.

		Wt[a]	CP[b]	Monoterpene[c]	
	n (%)	$\bar{x}$ (SE)	$\bar{x}$ (SE)	Total $\bar{x}$ (SE)	B[d] $\bar{x}$ (SE)
Nest Initiation					
Yearling	7 (64%)	1.13 (0.15)	16.41 (0.43)	7.20 (1.61)	0.94 (0.22)
Adult	12 (100%)	1.44 (0.05)	17.08 (0.61)	6.65 (0.68)	0.89 (0.14)
Combined	19 (83%)	1.31 (0.04)	16.84 (0.42)	6.86 (0.71)	0.91 (0.15)
Apparent nest success					
Successful	10 (53%)	1.41 (0.05)	16.73 (0.59)	7.37 (0.84)	1.18 (0.13)
Unsuccessful	9 (47%)	1.17 (0.18)	16.74 (0.66)	6.27 (0.77)	0.60 (0.13)

[a]Female body weight at time of capture (kg); excluding females captured in previous year
[b]Average percent crude protein
[c]Concentration of monoterpenes (mg/g)
[d]Individual unidentified monoterpene

concentration of black sagebrush samples by age of nesting females ($P > 0.05$). The nutrition and chemical content of black sagebrush sampled at browse sites was not related to the monthly survival rates of radio-marked female sage-grouse for March to May 2013 ($\beta = 0.03$, CI = -0.11–0.18) for average percent crude protein ($\beta = 0.14$, CI = -0.21–0.49) or total monoterpene concentration.

Discussion

The radio-marked female sage-grouse we monitored exhibited a higher probability of use for black sagebrush than big sagebrush subspecies, selecting the species at 73% of observed sites. Thacker et al. (2012) reported similar observations within the Box Elder SGMA, confirming only black sagebrush in 72% of winter sage-grouse pellets. Frye et al. (2013) reported that sage-grouse in south-central Idaho selected black sagebrush over Wyoming big sagebrush and suggested that black sagebrush was selected because of its lower total monoterpene concentration, despite the higher crude protein content of Wyoming big sagebrush.

We documented a higher crude protein in Wyoming big sagebrush than black sagebrush. We also documented lower total monoterpene concentrations in Wyoming big sagebrush than black sagebrush, which suggests that the radio-marked female sage-grouse we studied may have selected sagebrush species based on some unique aspect of an individual monoterpene rather than the total monoterpene concentrations. Our monoterpene concentrations may have differed from Frye et al. (2013) because of different sampling periods, as the phyto-chemistry of sagebrush can change seasonally (Kelsey et al. 1982, Striby et al. 1987).

Within our black sagebrush samples, we found no differences in total monoterpene concentrations between browsed, non-browsed, and non-browsed random sites. Remington and Braun (1985) and Frye et al. (2013) reported similar observations in total concentrations of monoterpenes. Frye et al. (2013) suggested that concentrations of individual monoterpenes, rather than the cumulative concentration, may determine the plants that sage-grouse select within black sagebrush patches. The difference in the concentration of 1 unidentified monoterpene (i.e., "B") between browsed black sagebrush plants support this conclusion.

Although our nest sample sizes were low and we only conducted a 1-year study, the fact that the observed differences in concentrations of monoterpene "B" were about twice as concentrated in samples associated with successful than unsuccessful females may be biologically significant (Figure 3). Only the radio-marked females we recorded in black sagebrush patches that exhibited the higher concentration of monoterpene "B" hatched their nests.

These results suggest that a higher concentration of monoterpene "B" in the black sagebrush stands where successful nesting female sage-grouse were observed may have provided them a selective advantage in terms of either pre-nesting condition or behavior. Though many PSMs have proven to negatively affect the fitness and productivity of herbivores, some studies have demonstrated that, at certain doses, potentially toxic PSMs can actually increase animal fitness by combating bacteria and parasites, stimulating increased vigilance, and aiding in thermoregulation (Forbey et al. 2009). It is possible that the monoterpene we observed in higher concentrations in association with successful females may have provided a positive benefit to their fitness and increased their probability of producing a successful nest. The dietary selections of these females may have enhanced their body condition or increased their nutrient reserves, which would allow them to spend less time away from their nest to forage and thus reduce their exposure to predators (Coates and Delehanty 2008).

It is also possible that female sage-grouse we studied selected black sagebrush over Wyoming big sagebrush based on some other aspect of nutritional or chemical content. Black sagebrush in the study area may also have contained other PSMs, nutrients, sugars, or fats that provided female sage-grouse with an increase of energy reserves to meet the demands of reproduction.

Previous studies have reported that forbs are also important in the diet of pre-nesting sage-grouse females (see Connelly et al. 2011 for review, Dahlgren et al. 2015*a*). Barnett and Crawford (1994) reported that the diet by dry weight of pre-nesting females that were shot and sampled in western Oregon consisted of 18–50% forbs (50–82% sagebrush). Gregg et al. (2008) reported that 89% of pre-nesting females that were shot and collected in southeastern Oregon and northwestern Nevada had forb tissue in their crops, and forbs comprised an average of 30% of their diet by dry weight. In comparison, sagebrush was found in 97% of crops and made up the remaining 70% of the female sage-grouse diet by dry weight. Only Gregg et al. (2008) reported insect taxa in the diet. We did not sample forbs or arthropods in the study area during the pre-nesting period of 2013 because neither were documented until the second week of April, when females began to nest. The delay in forb and arthropod appearance was related to the persistent snow cover and colder-than-average temperatures of the year. It is possible that we may not have detected some forbs and a limited number may have been available for sage-grouse use during the study period.

Because our radio-marked females were associated with sage-grouse flocks, and usually flushed 100 m from the approaching researcher (Thacker et al. 2012), we are only certain that the radio-marked individual was part of the flock and thus present at the browse sites. However, the sagebrush plants we observed and sampled could have been browsed by other members of the flock, and there may be some differences in forage selection patterns between individual sage-grouse of the same flock.

Wyoming big sagebrush communities provided pre-nesting browse sites for the radio-marked female sage-grouse in our study area. Wyoming big sagebrush may be of particular importance to wintering sage-grouse when snow levels rise above the lower canopy height of the black sagebrush, making it unavailable as forage. The greater height of Wyoming big sagebrush may also be critically important to this sage-grouse population for nesting or escape cover (Dahlgren et al. 2015*b*).

Management implications

Our research confirmed the importance of black sagebrush as pre-nesting female sage-grouse forage. Concomitantly, management actions in the winter and breeding ranges of sage-grouse in northwestern Utah should emphasize the conservation of black sagebrush along with big sagebrush species. Although we do not know the exact mechanism, our research also suggested that specific communities of black sagebrush may play a role in increased nest success in this sage-grouse population. Future research on sage-grouse winter foraging patterns may benefit from GPS transmitter technology, which would allow researchers to sample additional individual sage-grouse browse sites. Plant samples collected in direct association with individual marked sage-grouse will be needed to provide greater certainty regarding the potential effects of

the chemical and nutritional composition of pre-nesting foraging diets of sage-grouse on individual bird fitness and productivity.

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Brian R. Wing earned his B.S. degree in biology/zoology from Southern Utah University in 2009 and his M.S. degree in wildlife biology/management from Utah State University in 2014. His graduate research focused on the relationship between vegetation characteristics and sage-grouse vital rates. He currently works for the Utah Division of Wildlife Resources as a fish culturist.



Terry A. Messmer is a professor and extension wildlife specialist in the Department of Wildland Resources at Utah State University (USU). He holds the Quinney Professorship of Wildlife Conflict Management in USU's Quinney College of Natural Resources, and he is the director of USU's Utah Community-Based Conservation Program (CBCP) and the Jack H. Berryman Institute for Wildlife Damage Management. He received a B.S. degree in fisheries and wildlife management and biology from the University of North Dakota—Grand Forks, an M.S. degree in regional and community planning and a Ph.D. degree in animal and range science from North Dakota State University—Fargo. His research, teaching, and extension activities include identification, implementation, and evaluation of conservation strategies, technologies, and partnerships that can benefit agriculture, wildlife, and resources stakeholders.

