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Authors: Wanner, Caitlyn P., Pratt, Aaron C., and Beck, Jeffrey L.

Source: Rangeland Ecology and Management, 94(1) : 1-6

Published By: Society for Range Management

URL: https://doi.org/10.1016/j.rama.2024.01.008

Rangeland Ecology & Management 94 (2024) 1–6

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama

Original Research

Wintering Greater Sage-Grouse Preferentially Select Shrub Microhabitat Characteristics Within the Home Range

Caitlyn P. Wanner [1], Aaron C. Pratt [1,2], Jeffrey L. Beck [1,*]

[1] Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA
[2] George Miksch Sutton Avian Research Center, Bartlesville, OK 74005, USA

ARTICLE INFO

Article history:
Received 21 January 2023
Revised 8 December 2023
Accepted 19 January 2024

Key Words:
Centrocercus urophasianus
Dung counts
Home-range-scale microhabitat selection
Population-scale microhabitat selection
Shrubs
Winter habitat

ABSTRACT

In temperate landscapes, habitat selection is constrained by resource availability during winter. Most studies of habitat selection by greater sage-grouse (*Centrocercus urophasianus* "sage-grouse") have focused on breeding and summer rather than winter habitat. We focused on winter microhabitat when available habitat was influenced by snow conditions. Our objectives were to 1) identify what microhabitat characteristics sage-grouse select during winter and 2) evaluate whether sage-grouse selected microhabitat at the home range (third order) or the population range (second order) scale. In summer 2020, we measured shrub characteristics and herbivore dung counts at 90 sage-grouse locations from the previous 2019/2020 winter in northwest Colorado and southcentral Wyoming and compared them with 90 paired, available locations within sage-grouse home ranges and 90 unpaired, available locations within the population range. We found strong support for sage-grouse selecting for winter microhabitat at the home-range scale because we observed similar differences in shrub characteristics between sage-grouse use locations and available locations at both scales and no differences between randomly available habitat. Compared with available locations within home ranges, wintering sage-grouse selected areas of 57.1% greater big sagebrush (*Artemisia tridentata* spp. Nutt.) canopy cover, 23.7% taller big sagebrush, and 110.6% more visual obstruction at use locations. Sage-grouse dung piles were 7.1 × higher at used locations than available locations within home ranges, further indicating that habitat use was less random within home ranges. In winter, microhabitat selection focused on higher cover and height of big sagebrush like previous observations from nearby studies of microhabitat selected by sage-grouse during nesting and brood-rearing.

Introduction

Limited resource availability makes habitat selection during winter challenging for temperate wildlife species. Most studies of habitat selection by greater sage-grouse (*Centrocercus urophasianus* "sage-grouse") have focused on breeding and summer (Connelly et al. 2011) instead of winter habitat selection, especially for microhabitat (but see Hagen et al. 2011). We focused on microhabitat during winter when sage-grouse habitat selection is often limited to above-snow vegetation (mainly shrubs). We designed our study to characterize winter microhabitat selection at the population (second order) and home range (third order) scales (Johnson 1980). We had two research objectives. The first was to identify what shrub microhabitat characteristics sage-grouse select during winter. The second was to evaluate whether they were mostly selecting this habitat at the home- or population-range scale using habitat measurements at grouse-use locations, home-range available locations, and population-range available locations. We propose four possible hypotheses (and lines of evidence for each; Table 1) representing the scale of grouse habitat selection in our study: 1) no selection at either the home range or population scale, 2) selection predominately at the population scale (second order), 3) selection predominately at the home-range scale (third order), and 4) significant selection at both scales. Incorporating a multiscale hierarchical framework is the widely recommended method for studying habitat selection (Mayor et al. 2009), though it is often lacking in microhabitat studies (McGarigal et al. 2016). Information about winter habitat selection by sage-grouse will better inform conservation of this imperiled rangeland species.

* Correspondence: Jeffrey L. Beck, Dept of Ecosystem Science and Management, College of Agriculture, Life Sciences and Natural Resources, University of Wyoming, Dept 3354, Laramie, WY 82071, USA.
E-mail address: jlbeck@uwyo.edu (J.L. Beck).

https://doi.org/10.1016/j.rama.2024.01.008
1550-7424/

Table 1
Hypothetical example of possible outcomes for comparison of sagebrush cover at greater sage-grouse use, home range available, and population range available locations representing four hypotheses of scale of selection. In this example, grouse preferentially select for sagebrush cover.

Hypothesis	Use vs. home range available	Use vs. population available	Home range vs. population available
No selection at either scale	No difference	No difference	No difference
Selection at population scale	No difference	Cover higher at use	Cover higher at home range available
Selection at home range scale	Cover higher at use	Cover higher at use	No difference
Selection at both scales	Cover higher at use	Cover higher at use	Cover higher at home range available

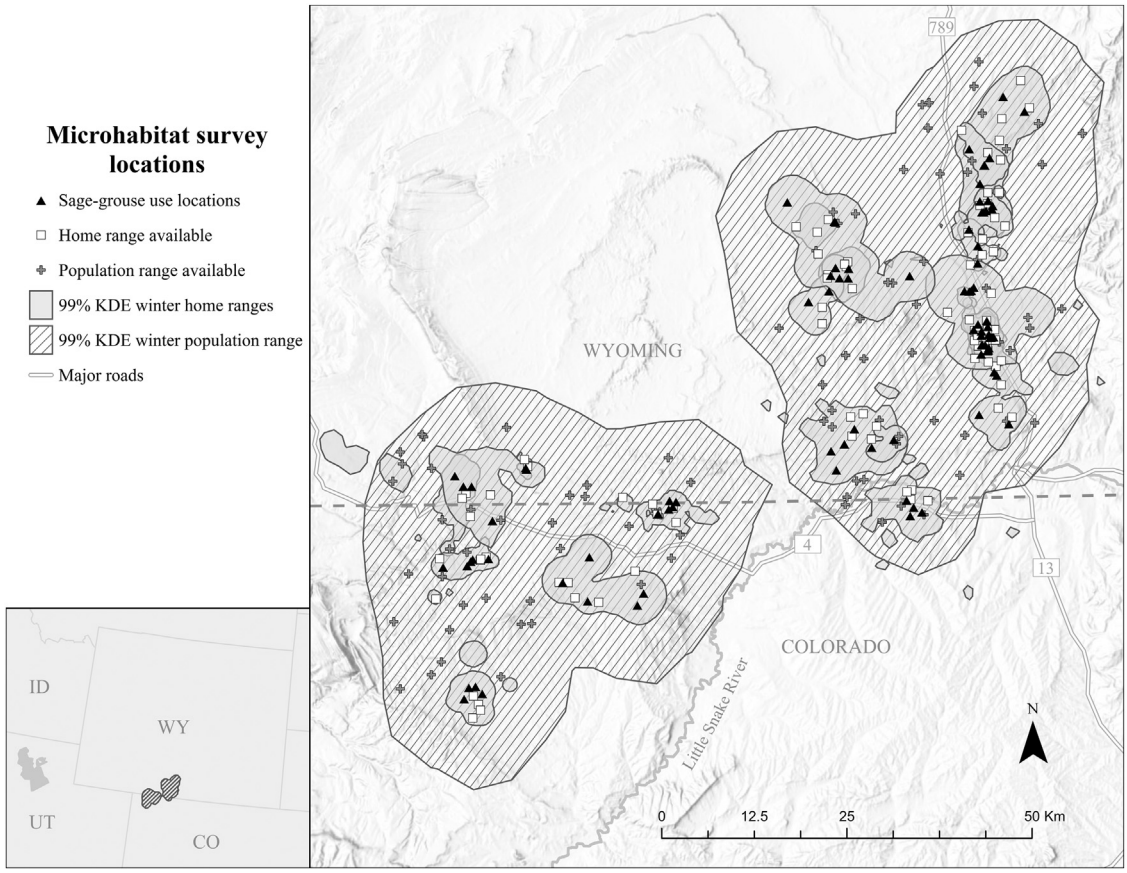

Figure 1. Study area map depicting locations of sage-grouse use and random available locations within home-range and population scales, southwestern Wyoming and northwestern Colorado, United States, winter 2019/2020. Home and population ranges estimated with a 99% kernel density estimator (KDE).

Methods

Study area

Our study area was located near the intersections of Sweetwater and Carbon counties, Wyoming, and Moffat County, Colorado, with 67% of the study area located in Wyoming (Fig. 1). The 4 660-km^2 study area was mostly composed of Bureau of Land Management–managed land (85%) and included private (10%) and state (5%) land. Our study area was categorized as cold arid-steppe (Kottek et al. 2006) with elevation ranging from 1 800 to 2 500 m (USGS 2016) and the 30-yr (1991–2021) mean core winter (1 Dec–28 Feb) precipitation ranged from 11.7 to 39.8 cm (PRISM Climate Group 2022). During the core months of winter 2019/2020, mean accumulated precipitation (24.3 cm) was in the 91st percentile compared with the 30-yr average and in the 31st percentile for mean winter temperature (−6.4°C; PRISM 2022). Sage-grouse locations were clustered in the flat, lower elevations at elevations between 1 850 and 2 200 m. Snow depth ranged from 0 to 48 cm with a mean of 19 cm at use locations, according to snow depth values modeled using SnoModel from our study period (Liston et al. 2020). In microhabitat plots we identified 21 shrubs to species or genera. Dominant shrubs included big sagebrush (*Artemisia tridentata* Nutt.), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), shadscale saltbush (*Atriplex confertifolia* [Torr. & Frém.] S. Watson), and yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.). We identified seven subshrub species, with birdsfoot sagebrush (*A. pedatifida* Nutt.), Gardner's saltbush (*Atriplex gardneri* [Moq.] D. Dietr.), and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit) most common.

Capture and monitoring

We captured and radiomarked adult female sage-grouse using spotlight and hoop-net methods (Giesen et al. 1982; Wakkinen et al. 1992) during all seasons of the year. Sage-grouse capturing and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266) and Wyoming Game and Fish Department Chapter 33-1160 permit. We fitted yearling and adult female sage-grouse with rump-mounted Global Positioning System (GPS) transmitters (22-g GPS PTT [GeoTrack, King George, VA] or 15-g Bird

Table 2
Mean (± standard of error) of winter microhabitat characteristics at locations used by sage-grouse, available locations within home ranges, and available locations within the population range. We recorded shrub characteristics and dung counts at winter 2019/2020 plots in summer 2020, northwest Colorado and southcentral, Wyoming, United States.

Microhabitat characteristics	Grouse use	Available	
		Home range	Population range
Dung counts (piles/400 m^2)			
Cattle	7.57 ± 0.79	4.86 ± 0.74	6.49 ± 1.16
Horse	3.29 ± 0.61	3.43 ± 0.70	3.90 ± 0.87
Native ungulate[1]	52.08 ± 4.24	51.75 ± 5.75	46.07 ± 4.49
Sage-grouse	14.80 ± 1.62	2.10 ± 0.48	1.49 ± 0.58
Canopy cover (%)			
Big sagebrush	24.25 ± 1.07	15.44 ± 1.22	12.14 ± 1.07
Nonsagebrush shrub	3.74 ± 0.60	3.85 ± 0.86	5.66 ± 0.75
Sub-shrub	0.86 ± 0.17	1.52 ± 0.30	2.82 ± 0.46
Overall (shrub + subshrub)	28.86 ± 1.03	20.81 ± 1.27	20.62 ± 1.14
Height (cm)			
Big sagebrush	37.82 ± 0.55	30.58 ± 0.41	33.48 ± 0.55
Nonsagebrush shrub	37.58 ± 0.96	30.21 ± 0.75	30.61 ± 0.84
Overall (shrub + subshrub)	35.01 ± 0.48	26.04 ± 0.39	26.61 ± 0.51
Other shrub attributes			
Shrub species richness (no.)	2.72 ± 0.15	2.81 ± 0.14	3.37 ± 0.19
Visual obstruction (dm)	1.79 ± 0.13	0.85 ± 0.08	0.98 ± 0.12
Sagebrush presence (0/1)	1.00 ± 0.00	0.94 ± 0.02	0.89 ± 0.03

[1] Native ungulates included elk, mule deer, and pronghorn.

Solar [e-obs GmbH, Grunwald, Germany], total weight ~32 g) that recorded at least four locations per day.

Microhabitat measurements

To obtain microhabitat conditions, we sampled vegetation at sage-grouse winter use locations from winter 2019/2020. We defined winter as 1 December–March 14 to be consistent with the Wyoming Greater Sage-Grouse Executive Order (State of Wyoming 2019), and we only used grouse location data within these dates if sage-grouse were confirmed to be on winter range based on movement behavior (Pratt et al. 2017). We used winter 2019/2020 snow depth data from the Cow Creek Wyoming weather station (Bureau of Land Management NWS ID 482011) to broadly categorize days between 1 December and 14 March as low, moderate, and high snow depth (0–25, 26–75, and 76–99 percentile, respectively). For each marked sage-grouse, we randomly selected a location from at least one day during each snow-depth period. This approach provided greater temporal independence between locations. For each use point we paired an available point randomly generated within that bird's winter home range, which we estimated using a 99% kernel density estimator in the "adehabitatHR" package of R (version 4.1.2; Calenge 2011; see Fig. 1). We estimated the population range using a 99% kernel density estimator for all bird locations and then randomly generated an equal number of available points at the population scale (see Fig. 1). In generating available locations, we first excluded any areas we defined as "nonhabitat" such as exposed rock, open water, human development, and forest (LANDFIRE 2016).

Sampling microhabitat locations during winter is not logistically feasible due to impassable roads, safety concerns for field personnel, disturbance to winter-stressed wildlife, and annual variability in snow depth that may limit field data collection only to accessible areas. We also assumed that measuring average shrub characteristics during summer is more comparable with spatial products, which are based on summer measurements (e.g., Xian et al. 2015). To assess the assumption that shrub heights measured during summer would be correlated with heights measured during winter, we compared shrub height measurements taken from National Land Cover Database remotely sensed products (Xian et al. 2015) at sage-grouse locations and overlaid them with average snow level synthesized from SnowModel (Liston et al. 2020). When we paired base shrub height with mean protruding shrub height above snow at 16 376 sage-grouse locations across winters 2018/2019 and 2019/2020, we found a Pearson's correlation coefficient (r) of 0.573 ($t_{16,374} = 89.4$, P value <0.001). This assessment with remotely sensed data confirmed our assumption that shrub heights measured with and without snow are correlated. Further, measuring shrubs during snow-free periods is most practical because snow depth constantly changes within and between years, making winter sampling prone to mismatches between shrub characteristics sage-grouse encountered when they used locations and the dates those locations are sampled. Furthermore, postwinter sampling of sagebrush characteristics is measurable by managers (Connelly et al. 2000). Thus, during summer 2020 (26 May–20 August), we visited each location to measure shrub characteristics and dung counts at microhabitat plots. We did not measure herbaceous vegetation because sage-grouse consume sagebrush exclusively in winter (Wallestad and Eng 1975) and select winter microhabitat for shrub-meditated structural characteristics and nutritional quality (Hagen et al. 2011; Frye et al. 2013).

We assessed winter microhabitat characteristics at sage-grouse use and available plots using two 50-m transects (100-m total) that intersected at the center and extended in the cardinal directions. We defined subshrubs as shrub species with typical height at maturity <3 dm. We measured canopy cover by species along each 50-m transect using the line-intercept method (Canfield 1941). Every 2.5 m along the transect line, we recorded the height of the nearest shrub. To estimate species richness, we recorded every shrub to species or genus rooted within 1 m of the right side of each transect line (100 m^2 total). Shrub characteristics included overall shrub height (shrubs and subshrubs combined), big sagebrush height, nonsagebrush height (shrubs and subshrubs combined), overall canopy cover (all shrubs and subshrubs), sagebrush canopy cover, nonsagebrush shrub canopy cover, subshrub canopy cover, species richness, and whether big sagebrush was present (0 or 1) at the location (Table 2). We considered big sagebrush separately because it is the most important attribute characterizing sage-grouse winter habitat (Connelly et al. 2011; Dzialak et al. 2013; Smith et al. 2014, 2021). We used a Robel pole to measure visual obstruction to the nearest 0.5 dm by visually observing shrub obstruction of the pole from 4 m away and 1 m from the

ground along the transect at 0-, 10-, 15-, 20-, 25-, 30-, 35, 40-, and 50-m intervals (Robel et al. 1970).

At each sampling location we recorded piles of dung from sage-grouse, native ungulates (elk [*Cervus elaphus*], mule deer [*Odocoileus hemionus*], and pronghorn [*Antilocapra americana*]); free-roaming horses (*Equus ferus caballus*); and cattle within 2 m on each side of each 50-m transect line (400 m^2 total). For dung piles to represent general degree of use during winter, we did not include fresh dung that we considered to be deposited after spring. We recorded dung piles as a signal to verify relative use by sage-grouse and to compare grouse use of the landscape with that of ungulate use during the winter.

Statistical analysis

For each habitat variable we conducted three comparisons: grouse use versus home range available, grouse use versus population range available, and home range available versus population range available (see Table 1). Within home ranges, we compared vegetation characteristics and dung counts between sage-grouse use locations and home range available locations using paired *t*-tests. We used two-sample *t*-tests to compare the means of microhabitat characteristics at used and home range available locations to those characteristics measured at population range available locations. We used chi-square tests to compare presence of big sagebrush at sage-grouse use locations compared with available locations within home and population ranges. We conducted all statistical analyses in R and set statistical significance at alpha = 0.05. We adjusted *P* values generated for *t*-tests and chi-square tests using the Bonferroni correction to correct the experiment-wise error rate inherent in multiple tests (Dunn 1961). We report effect sizes as Cohen's *d* for *t*-tests, Cohen's *g* for paired chi-square tests, and Cohen's *w* for unpaired chi-square tests (Cohen 1992). If there were no significant difference results for all three tests, then we interpreted that as evidence for the hypothesis that grouse were not selecting habitat relative to that variable at either the population- or home-range scale (see Table 1). Population-scale selection is selecting home ranges within habitat available to the greater population. The home range available locations represented habitat within grouse home ranges, so we interpreted significant differences between home range available and population range available habitat as evidence for habitat selection at the population scale. Grouse use locations represented the habitat used within grouse home ranges, so we interpreted significant differences between grouse use habitat and home range available habitat as evidence for selection at the home range scale. The collective results for the three tests provided evidence for which scale of habitat selection hypothesis best matched our observations (see Table 1). If results of the three tests did not match one of our four proposed hypotheses, then we interpreted it as inconclusive evidence.

Results

We used 90 use locations from 24 GPS−marked sage-grouse, 90 home range available, and 90 population available locations (see Fig. 1). With a statistical significance of 0.05 (Bonferroni-corrected significance = 0.01667) and statistical power of 0.80, this sample size allowed us to detect medium and larger effect sizes (Cohen's $d \approx 0.34$). Five of 10 shrub characteristics measured—height and canopy cover of big sagebrush and overall shrubs, and visual obstruction—were greater at use locations compared with available locations within the home range (Tables 2 and 3). At grouse-use locations, big sagebrush canopy cover and height were 57.1% and 23.7% greater, respectively, compared with available locations within the home range (see Table 2). At use locations, visual obstruction was 110.6% greater than within the home range (see Table 2).

Five of the 10 shrub characteristics measured—canopy cover of big sagebrush and overall shrubs, height of big sagebrush, visual obstruction, and probability of big sagebrush presence—were greater at use locations compared with available locations within the population range (see Tables 2 and 3). Big sagebrush canopy cover was 99.8% higher at use locations compared with available population-scale locations (see Table 2). Big sagebrush height and visual obstruction were 13.0% and 82.7% higher at use locations compared with available population-scale locations (see Table 2). In contrast, two shrub characteristics, subshrub canopy cover and shrub species richness, were 69.5% and 19.3% lower at use locations than at available population-scale locations (see Table 2).

We found no difference (0 of 10 characteristics) in shrub characteristics or dung counts between available locations within the home range compared with the population range (see Table 3) for sage-grouse or any ungulate. Sage-grouse dung counts at use locations were 7.1 × greater compared with home range available locations and 9.9 × greater compared with population range available locations (see Table 2). Higher use of these areas by sage-grouse rather than ungulates further confirmed higher use of these winter sites, specifically by sage-grouse and mostly irrespective of ungulate use (see Tables 2 and 3). The pattern of grouse use relative to cattle use was inconclusive (see Table 3).

Of the eight habitat microhabitat features for which we observed significant selection, four provided evidence for the hypothesis that sage-grouse were selecting these features within the home-range scale (see Tables 1–3). For the other four features the evidence was inconclusive. The variation in sage-grouse dung was similar, further suggesting that habitat use was less random within home ranges.

Discussion

We found a lack of differences in microhabitat characteristics between random available locations at the population and home range scales, suggesting that sage-grouse selected home ranges with similar microhabitat as what was widely available within the population range. However, significant differences between use locations and available locations at both scales (and the direction and magnitude of the differences between use and available locations were similar) indicate that sage-grouse selected winter microhabitat within the home-range scale over the population scale. Microhabitat studies frequently either compare use locations with available locations within the home range or to available locations across the study area (e.g., Dinkins et al. 2016). In our study, both comparisons gave similar conclusions on identifying the habitat features sage-grouse were selecting (there were inconsistent conclusions for 4 of 10 features) because when the grouse were selecting winter home ranges, on average, the microhabitat within home ranges was like that in the greater population range. The conclusion of grouse selecting microhabitat at the home-range scale may not hold in other study areas, so it is worth repeating. Without previous studies collecting data on available habitat at multiple scales, it is not possible to parse out what scale sage-grouse were selecting habitat in those study areas. Sage-grouse conservation efforts designed at the population scale may unintendedly assume approximate homogeneity within home ranges. Selection for shrub microhabitat at the home range scale supports management of shrub characteristics within home range scales.

Our microhabitat results demonstrated the reliance of sage-grouse wintering in this region of Wyoming for taller sagebrush and greater sagebrush canopy cover consistent with findings from resource selection function models using remotely sensed shrub data in the same region (Dzialak et al. 2013; Smith et al. 2014,

Table 3
Paired *t*-tests for microhabitat characteristics and dung counts between grouse-use locations and paired home range randomly available plots. Student's *t*-tests comparisons between population range available plots and home range available and use plots. We used McNemar's chi-square (χ^2) test to assess presence of big sagebrush between paired grouse-use locations and home range available plots and Pearson's χ^2 test to compare unpaired available plots. We recorded microhabitat characteristics and dung counts at winter 2019/2020 habitat plots in summer 2020, northwest Colorado and southcentral, Wyoming, United States. **Bolded** *P* values are significantly different at alpha = 0.05.

Microhabitat characteristics	Grouse use versus random home range				Grouse use versus random population range					Random home range versus random population range				
	diff.[1]	*d*[2]	*t*[3]	*P*[4]	diff.	*d*	*t*	DF	*P*	diff.	*d*	*t*	DF	*P*
Dung counts (piles/400 m^2)														
Cattle	2.71	0.29	2.78	**0.020**	1.08	0.11	0.77	156.9	1.000	−1.63	0.18	−1.19	151.1	0.711
Horse	−0.14	0.02	−0.21	1.000	−0.61	0.09	−0.58	160.0	1.000	−0.47	0.06	−0.42	170.4	1.000
Native ungulate[5]	0.34	0.01	0.05	1.000	6.00	0.15	0.98	177.6	0.992	5.66	0.12	0.78	167.5	1.000
Sage-grouse	12.70	0.79	7.49	**<0.001**	13.31	1.15	7.72	111.2	**<0.001**	0.61	0.12	0.81	171.9	1.000
Canopy cover (%)														
Big sagebrush	8.81	0.62	5.92	**<0.001**	12.12	1.19	7.99	178.0	**<0.001**	3.31	0.30	2.04	175.3	0.128
Nonsagebrush shrub	−0.11	0.01	−0.11	1.000	−1.92	0.30	−2.00	168.9	0.142	−1.81	0.24	−1.58	175.1	0.347
Subshrub	−0.66	0.21	−2.00	0.146	−1.96	0.60	−4.03	112.9	**<0.001**	−1.30	0.35	−2.38	154.7	0.056
Overall (shrub + subshrub)	8.04	0.56	5.31	**<0.001**	8.24	0.80	5.35	176.0	**<0.001**	0.20	0.02	0.11	176.2	1.000
Height (cm)														
Big sagebrush	10.15	0.51	4.79	**<0.001**	8.56	0.51	3.42	170.7	**0.002**	−1.59	0.09	−0.61	175.5	1.000
Nonsagebrush	4.43	0.15	1.40	0.494	−0.05	0.00	−0.01	150.9	1.000	−4.48	0.17	−1.11	155.6	0.810
Overall (shrub + subshrub)	9.87	0.53	5.00	**<0.001**	7.00	0.34	2.26	135.6	0.076	−2.87	0.14	−0.94	131.1	1.000
Other shrub attributes														
Shrub species richness	−0.09	0.05	−0.49	1.000	−0.64	0.40	−2.71	168.3	**0.022**	−0.56	0.35	−2.37	165.5	0.057
Visual obstruction (dm)	0.94	0.65	6.13	**<0.001**	0.81	0.68	4.55	176.1	**<0.001**	−0.13	0.13	−0.88	159.0	1.000
	diff.	*g*	χ^2[2]	*P*[6]	diff.	*w*	χ^2[2]	DF	*P*[7]	diff.	*w*	χ^2[2]	DF	*P*[7]
Big sagebrush presence (0/1)	0.06	0.50	3.20	0.221	0.11	0.24	8.58	1	**0.010**	0.06	0.10	1.16	1	0.842

[1] Diff indicates difference.
[2] *d* indicates Cohen's *d; g,* Cohen's *g; w,* Cohen's *w.*
[3] All degrees of freedom were 89 for paired *t*-tests.
[4] We adjusted *P* values from all tests with the Bonferroni correction.
[5] Native ungulates included elk, mule deer, and pronghorn.
[6] χ^2 test statistics and *P* values from McNemar's chi-squared test for symmetry between paired groups. Note: DF (degrees of freedom) is 1 for McNemar's chi-square tests.
[7] χ^2 test statistics and *P* values from Pearson's chi-square test of independence.

2021). In some regions, sage-grouse were reported to prefer areas with shorter sagebrush species (low sagebrush [*A. arbuscula* Nutt.], Hagen et al. 2011; black [*A. nova* A. Nelson], Frye et al. 2013) if snow levels did not exceed vegetation height (Hanff et al. 1994). Sage-grouse have also been reported to use taller sagebrush species during above-average snow levels (Hupp and Braun 1989; Hanf et al. 1994). Though our study did not account for snow depth outside of location sampling methods (our sampling included low, moderate, and high snow depths at the 91st percentile compared with 30-yr average; PRISM 2022), we found less variation around sagebrush characteristic means at use locations compared to available locations (see relative size of standard errors to means in Table 2), suggesting, that sage-grouse selected similar heights of sagebrush regardless of snow depth. Our results support previous conclusions that sage-grouse can be expected to find microhabitat with favorable structural characteristics within winter home ranges despite changing snow patterns in average winters (Connelly et al. 2000). Like previous observations in nearby study areas of microhabitat selection during nesting and brood-rearing, sage-grouse selected winter microhabitat with greater canopy cover, visual obstruction, and shrub height (Kirol et al. 2012; Dinkins et al. 2016). These results indicate concealment cover is important to sage-grouse throughout their annual cycle. However, Gelling et al. (2022) showed, at least during the brood-rearing season, that microhabitat selected by sage-grouse can vary depending on reproductive state and behavioral state, even to the extent that a habitat characteristic can be both selected for and avoided depending on the time of day. Therefore, land managers in landscapes used by grouse during multiple seasons during the year should maintain sage-grouse habitat with diverse age structures within home ranges.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank personnel from the Wyoming Game and Fish Department and Rawlins Field Office of the Bureau of Land Management for logistical support. We thank private landowners for access to their lands to conduct our research. We thank K. Smith and J. Hennig for assistance with capturing grouse and A. Kross and R. Nielson for assistance in collecting field data.

The Sublette County Conservation District, University of Wyoming–Agricultural Experiment Station, Wyoming Game and Fish Dept, Wyoming Local Sage-Grouse Working Groups (South-Central, Southwest, and Wind River/Sweetwater River), and Wyoming State Office of the Bureau of Land Management (grant L17AC00272) funded our research.

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