

CONTRIBUTED PAPER

The influence of a conservation-based grazing program on greater sage-grouse habitat selection

Jennifer E. Helm^{1,2}  | Elizabeth G. Simpson¹  | Lorelle I. Berkeley³ |
Mark Szczypinski³ | Shea P. Coons¹ | Victoria J. Dreitz¹ 

¹Avian Science Center, Wildlife Biology Program, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, Montana, USA

²USDA Forest Service Rocky Mountain Research Station, Missoula, Montana, USA

³Montana Fish, Wildlife and Parks, Helena, Montana, USA

Correspondence

Jennifer E. Helm, USDA Forest Service
Rocky Mountain Research Station,
800 East Beckwith Avenue, Missoula, MT
59801, USA.
Email: jennifer.helm@usda.gov

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Abstract

Understanding how vegetation management affects animals' habitat selection patterns is critical for comprehensive conservation planning. As part of a decade-long study (2011–2019) of 486 adult female sage-grouse in central Montana, we investigated how a conservation-based grazing program (CGP) affected greater sage-grouse (*Centrocercus urophasianus*) habitat selection at two temporal scales: (a) the seasonal scale (four biologically relevant seasons) and (b) the annual scale. We used resource selection functions to assess sage-grouse selection for pastures enrolled in a CGP as well as plant functional type and topography. We found that sage-grouse strongly selected shrub cover, flatter slopes, and less tree cover. They selected CGP-enrolled pastures (Pre-, During-, and Post-grazing system implementation) over Non-CGP pastures during all seasons except the summer–fall. During the summer–fall, they selected pastures where CGP implementation was complete. Future research is needed to determine whether selection for CGP-enrolled pastures was due to unmeasured, underlying differences between CGP and non-CGP pastures or CGP enrollment patterns rather than effects of different grazing systems, as well as whether these habitat selection differences are linked to demographic rates or population dynamics.

KEYWORDS

Centrocercus urophasianus, rangeland management, resource selection, sage-grouse initiative

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1 | INTRODUCTION

Understanding the decisions animals make about where to distribute across the landscape provides key information about their ecology (e.g., Catchpole, 1974; Hildén, 1965; Lack, 1933) and habitat needs (Caughley, 1994). Habitat selection, the disproportionate use of resources or conditions by living things (Manly et al., 2002), involves animals interacting with their environment as they weigh scale-specific trade-offs between rewards and risks (Mayor et al., 2009). For example, an animal may decide where and when to forage based on the spatiotemporal distribution of predation risk (Mayor et al., 2009) and the variability of food resources (e.g., Donnelly et al., 2019; Previtali et al., 2009). Therefore, conservation practitioners, including private landowners, land managers, and wildlife managers, need information about the spatial and temporal dynamics of habitat selection to prioritize conservation actions.

The spatiotemporal dynamics of habitat selection are especially important for species like greater sage-grouse (*Centrocercus urophasianus*, hereafter “sage-grouse”), where decline is associated with habitat loss, including fragmentation and degradation (Connelly et al., 2004). Sagebrush (*Artemisia* spp.), a critical component of sage-grouse habitat, has been reduced to 55% of its historical extent due to varying threats across its range (Miller et al., 2011). Sage-grouse habitat loss and fragmentation have resulted from both direct and indirect factors, including conversion to cropland (Foley et al., 2011), cheatgrass invasion (Bradley et al., 2018), conifer encroachment (Aldridge et al., 2008; Davies et al., 2011), and energy and urban development and infrastructure (Asner et al., 2004; Connelly et al., 2004; Naugle, 2011). Indirect effects of habitat conversion can alter ecosystem processes, which create additional management challenges (West, 1983; West & Hassan, 1985; Wroblewski & Kauffman, 2003). For example, in the past, overgrazing by domestic livestock contributed to sagebrush habitat conversion and interacted with other factors to alter vegetation communities throughout the sage-grouse range (Cooper, 1960; Fleischner, 1994). Since habitat changes play a major role in sage-grouse decline, it is important to understand how habitat selection varies in relation to local habitat stressors to inform effective management.

Assessing habitat selection across seasons can provide a nuanced and comprehensive understanding of how sage-grouse respond to land uses (e.g., energy development) and management strategies (Aldridge & Boyce, 2007; Carpenter et al., 2010; Connelly et al., 1988; Doherty et al., 2008). Seasonal partitioning of habitat by sage-grouse often occurs even in the absence of migration (Dinkins et al., 2017; Fedy et al., 2012; Wallestad, 1975) and reflects variable needs for protection from predators

and inclement weather while also meeting forage requirements (Dinkins et al., 2014; Eng & Schladweiler, 1972; Gibson et al., 2017; Gregg et al., 1994; Pennington et al., 2016). Assessing habitat selection across seasons can also identify habitat characteristics with year-round importance, like sagebrush shrub cover, which female sage-grouse (hereafter “hens”) select during the spring nesting season (e.g., Smith et al., 2018b), late brood-rearing season in late summer to early fall (e.g., Braun et al., 2005), and winter (e.g., Connelly et al., 2000; Fedy et al., 2014). Comparing seasonal habitat selection to annual habitat selection can provide information to managers about the optimal timing of management actions in the context of what sage-grouse select year-round.

One such management action is the application of livestock grazing to pastures to achieve goals related to vegetation or livestock production. Grazing is ubiquitous across the sage-grouse range, but its effects on vegetation vary seasonally and regionally depending on the soil, weather, and vegetation type (Chambers et al., 2017; Lipsey & Naugle, 2017) and on the specific range management practices (e.g., adjusting grazing location and timing). Varied livestock grazing intensity across space and time may provide sage-grouse with a mosaic of herbaceous vegetation heights and growth stages (Davies et al., 2014), thereby affecting habitat selection patterns. For example, depending on the season, grazing could reduce grass cover at potential nest sites (Gibson et al., 2016; Smith et al., 2018b). Grazing when plants are not actively growing can decrease the height of some vegetation types (Davies et al., 2015) or lead to nutrient-rich new growth of fall-season herbaceous plants (e.g., Belsky, 1986, 1987) that serves as food for hens until snowfall.

Despite the prevalence of grazing throughout the sage-grouse range and the potential effects of grazing on sage-grouse, few studies have assessed the effect of grazing on sage-grouse habitat selection. We addressed this knowledge gap using a conservation-based grazing program (“CGP”) implemented as part of the “Sage Grouse Initiative” (Natural Resources Conservation Service [NRCS], 2015), a multipronged conservation program run by the NRCS in partnership with other federal and state agencies and private landowners. The CGP was intended to simultaneously maintain livestock production, rangeland health, and sage-grouse habitat through a voluntary rest-rotation or deferred grazing system tailored to pastures containing potential sage-grouse habitat, as indicated by areas of high sage-grouse abundance (Smith et al., 2018b).

We assessed whether differences between CGP and Non-CGP grazing practices yielded shifts in hen habitat selection across two temporal scales: (a) the seasonal

scale, divided into four life-stage related seasons—nesting, brood-rearing, summer-fall, and winter, and (b) the sage-grouse annual cycle from 2011 to 2019. We investigated whether hens selected different grazing program characteristics, vegetation cover (i.e., plant functional type), and topographic characteristics at the seasonal and annual temporal scales. We explored the effects of vegetation cover (shrub, annual, perennial, litter, bare ground, and tree) and topography (aspect, slope, and elevation) on habitat selection because these variables are linked to both habitat selection and demographic rates (e.g., Baxter et al., 2017; Beers & Frey, 2022). This study provides information about how CGP grazing practices affect sage-grouse habitat selection and may inform how managers weigh trade-offs when implementing grazing to achieve wildlife habitat objectives.

2 | METHODS

2.1 | Study area

The study area covered approximately 1500 km² in central Montana, USA, roughly centered on the town of

Roundup (Figure 1). All work was conducted in Musselshell, Golden Valley, Petroleum, and Wheatland counties, where rolling topography ranged from 975 to 1250 m in elevation (Smith et al., 2018a). Vegetation cover was dominated by perennial bunchgrasses, rhizomatous grasses, and forbs, along with a mix of shrubs—primarily Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and silver sagebrush (*Artemisia cana*)—and annual grasses and forbs. The average monthly temperature in Roundup (2009–2020) ranged from −3.8°C in January to 21.8°C in July (National Centers for Environmental Information, 2021) and average monthly precipitation (2009–2020) ranged from 9.40 mm in January to 73.41 mm in June (National Centers for Environmental Information, 2021). The climate is cold semiarid (Pyke et al., 2015), with distinct seasons that include cool and wet springs, hot and dry summers, cool and wet autumns, and cold, snowy winters. Most of the land is privately owned and used as rangeland for cattle and sheep and for dryland farming; however, it is intermixed with federal, state, and county land (Smith et al., 2018a, 2018b), which is also grazed. The study area encompassed 30 sage-grouse lekking areas (Smith et al., 2018a).

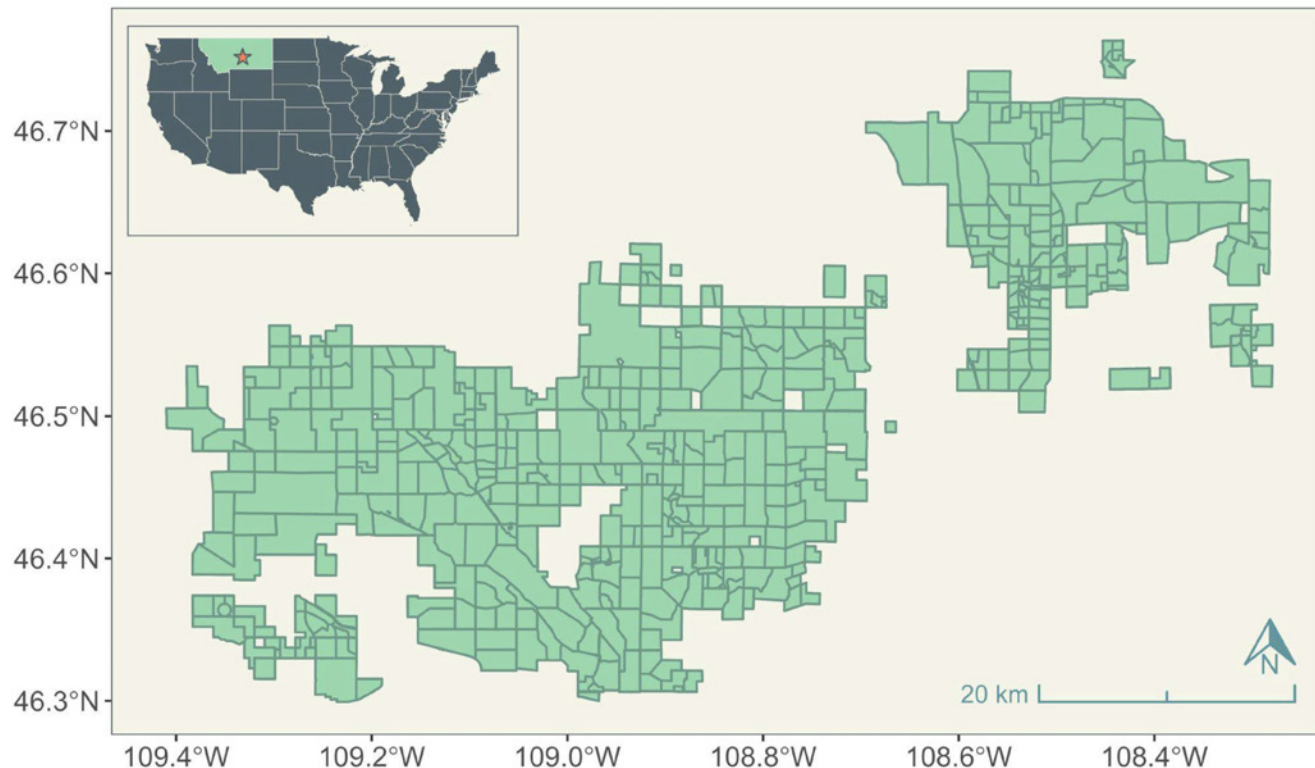


FIGURE 1 Greater sage-grouse were studied in an area encompassing 1500 km² (red star) in central Montana (lighter-colored state in the inset map) in the United States (inset map). The polygons in the main map represent the fenced boundaries of pastures where domestic livestock were grazed, and for which information about the grazing system was available (i.e., 10 years of grazing records for many—but not all—of these pastures). Some of these pastures were enrolled in a conservation-based grazing program through the Sage Grouse Initiative. Areas without mapped livestock pastures were likely grazed by domestic livestock and might be fenced, but detailed grazing information about these areas was unavailable.

2.2 | Sage-grouse hen capture and monitoring

In March and April 2011–2019, we used night-time spotlighting to capture hens on or near leks (Giesen et al., 1982; Wakkinen et al., 1992). We fitted hens with a 25 g necklace-style very high frequency (VHF) transmitter (Model A4060, Advanced Telemetry Systems, Isanti, MN) or a 25 g solar Global Positioning System (GPS) Platform Transmitter Terminal (PTT) (GeoTrax, Inc., Apex, NC, 22 g solar GPS, 2019 only). After capturing an initial sample of 100 hens in March and April 2011, we captured hens annually to replace lost or dead hens in an effort to maintain a sample size of ~100 hens. The number of unique hens tracked during each sage-grouse year ranged from 81 (2018) to 126 (2012) with a mean of 109 hens per year. We attempted to recapture hens in the fall after 2 years to replace transmitters before failure. Capturing and handling of sage-grouse hens was approved by the University of Montana's Institutional Animal Care and Use Committee protocols (AUP 009-18VDWB-031418; AUP 011-14DNWB-031914).

Monitoring methods and intervals varied based on both survey constraints and the biologically meaningful seasons we delineated based on sage-grouse life history. We defined four seasons as nesting (April 1–May 31), early brood-rearing (June 1–July 15, hereafter “brood-rearing”; Rice et al., 2016), late brood-rearing summer-fall (July 16–November 30, hereafter “summer-fall”; Rice et al., 2016; Walker et al., 2016), and winter (December 1–March 31; Walker et al., 2016). Detailed monitoring methods and sample sizes are described in Appendix 1, Supporting Information S1 and Table S1.

2.3 | Landcover and topography variables

We used remotely sensed ground cover and topography layers to determine habitat characteristics at each hen location because collecting on-the-ground field measurements of these covariates across all four seasons was not logistically feasible. For each year, we obtained estimates of plant functional types and abiotic conditions (% cover of shrub, annual forb and grass, perennial forb and grass, bare ground, tree, and litter) from the Rangeland Analysis Platform (annual temporal and 30-m spatial resolution, <https://rangelands.app/products/>; Allred et al., 2021; Jones et al., 2018) via Google Earth Engine (Gorelick et al., 2017).

We derived topographic variables (elevation, slope, and aspect) from the National Elevation Dataset (10-m spatial resolution, The National Map, United States

Geological Survey, <https://apps.nationalmap.gov/downloader/>). We downloaded six elevation tiles and then merged and clipped them to the study area in ArcMap (ESRI, 2020). We used the *raster* package (Hijmans, 2022) in program R to resample the tiles to match the plant functional type layers and derived slope and aspect from each point's eight nearest neighbors. Data summaries for key vegetation and topographic variables are in Figure S1 and Appendix 1, Supporting Information S1.

2.4 | Grazing program variables

Starting in 2011, the NRCS worked with private landowners to implement voluntary, incentivized, rest-rotation grazing systems (a conservation-based grazing program, or “CGP”) on pastures containing potential sage-grouse habitat, determined by topography and sagebrush canopy cover $\geq 5\%$ (NRCS personal communication, fall 2019). Ranches enrolled in the CGP were located within two state-designated core areas of high sage-grouse abundance. For each ranch enrolled in the CGP, a prescribed grazing plan implemented grazing in CGP pastures over three consecutive years that maintained moderate stocking rates, shifted grazing timing each year, and limited grazing durations (NRCS, 2017; Smith et al., 2018a). Each CGP grazing plan met the following criteria intended to support sage-grouse habitat: (1) utilization rates were $\leq 50\%$ of the current year's key forage species growth, (2) the grazing duration was ≤ 45 days at a time, (3) the timing of grazing changed by ≤ 20 days per year, and (4) there was a contingency plan for exceptional circumstances like drought or fire (NRCS, 2017; Smith et al., 2018a). CGP enrollment status was recorded at an annual temporal scale (Figure S2), and pastures during a given year were categorized as either non-CGP or CGP (further classified as Pre-CGP, During-CGP, and Post-CGP). Non-CGP grazing systems in the study area ranged from continuous grazing throughout the year to rotational grazing systems (Appendix 1, Supporting Information S1).

2.5 | Habitat selection analyses

We conducted five time-period-specific habitat selection analyses (nesting season, brood-rearing season, summer-fall season, winter season, and annual) using resource selection functions (RSFs) in a used-available framework (Manly et al., 2002). Used-available RSFs provide estimates of “relative probability of selection” (hereafter “selection”). We defined used points as locations of sage-

grouse occurrence, recorded using a variety of monitoring methods (ground-based VHF nest, chick, and hen monitoring; aerial VHF hen and chick monitoring; GPS hen monitoring). We defined available points as locations within each time-period-specific home range, as estimated by a 95% kernel density estimator (KDE), assuming that all areas within that region were available to be selected. Available points are locations that hens had the option to use; they may or may not actually be selected by hens (Johnson et al., 2006; McLoughlin et al., 2006). We conducted all analyses in Program R (R Core Team, 2020) and denote R packages in italics.

Available points were sampled from a 95% KDE that corresponded with one of the five time periods (*adehabitatHR*; Calenge & Fortmann-Roe, 2023). The 95% KDE is a preferred method for home range estimation (Laver & Kelly, 2008; Orning & Young, 2016; Powell, 2000). For each KDE, we pooled used points across all hens (Manly et al., 2002) present during the time period of interest (Figures 2 and S3a). For each used location, we sampled

10 available locations from the applicable 95% KDE to comprehensively represent the habitat available for hens. A ratio of 10 available points per used point balances the trade-off between sample size and computation time (Northrup et al., 2013). We randomly assigned each available point to an individual and a dataset from the pool present in each time period of interest. We stratified available points by year to account for variation in habitat selection across years (Picardi et al., 2020). We extracted all variables—vegetation (year-specific percent plant functional type cover), topography (constant during study period), and grazing (year-specific)—using *raster::extract* at both used and available points. We then pooled points across years within each of the five time periods.

For each of the five time-period-specific model sets, we conducted a variable screening process. We ran multivariate correlation tests (*GGally*; Schloerke et al., 2024) on the vegetation and topography variables and retained all variables of interest because $|r| < 0.5$ in all cases. For each model set, we ran univariable binomial logistic

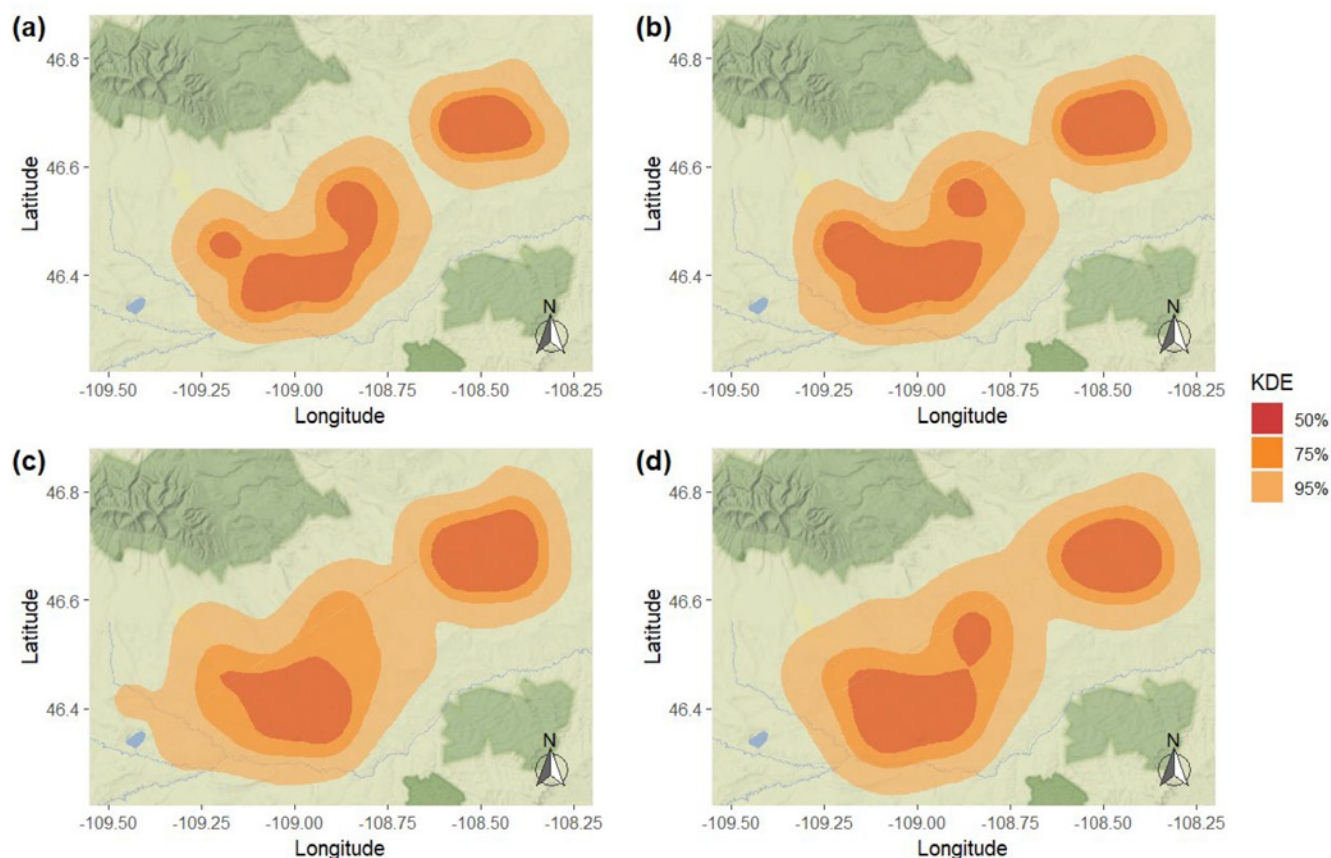


FIGURE 2 Greater sage-grouse hens in central Montana displayed slight spatial variation in seasonal home ranges, as represented by 95% kernel density estimates (KDEs) (light orange), 75% KDEs (bright orange), and 50% KDEs (dark orange), across four seasons: (a) nesting (April 1–May 31), (b) brood-rearing (June 1–July 15), (c) summer–fall (July 16–November 30), and (d) winter (December 1–March 31). The 95% KDE was most similar across seasons, whereas the 50% KDEs (the seasonal areas of higher concentrations) were most variable.

regressions using each of the nine candidate predictors (elevation, slope, aspect, shrub, bare ground, annual forb and grass, perennial forb and grass, tree, and litter). We compared univariable models to the null (intercept-only) model using the Akaike Information Criterion for small samples (AIC_c ; Akaike, 1973) and removed any variables whose AIC_c was higher than the null model. We also excluded variables if the 95% confidence interval (CI) around the coefficient estimate crossed 0.0. For each model set, this yielded a set of candidate variables that we carried forward to the next step.

Our model screening process eliminated very few variables across all model sets. As such, to avoid overfitting, we used a sequential process (Arnold, 2010; Smith et al., 2019). From this point forward, we centered and scaled all continuous variables to improve model convergence by subtracting the mean value of the variable and dividing by the standard deviation. We subset the remaining candidate fixed effects variables into three categories: vegetation, topography, and grazing. Within the vegetation and topography categories, we compared all additive combinations using AIC_c (*MuMIn*; Barton, 2009) and retained models within 2 AIC_c of the top model (Burnham & Anderson, 2002). For each of the five time-period-specific model sets, only a single model was competitive.

Next, we developed mixed-effects RSFs (implemented as binomial generalized mixed models) (*lme4*; Bates et al., 2015) to account for two study design constraints: (1) variation in the dataset, including the number of points and the monitoring method, and (2) variation in the number of points per individual (Gillies et al., 2006; Hebblewhite & Merrill, 2008) for each of the five time periods. Data included in these models were derived from four datasets—nest monitoring, chick monitoring, VHF-monitored hens, and GPS-monitored hens—and each dataset contains points from multiple seasons, meaning that multiple datasets were used for each model. We began with the top fixed effects model identified in the previous step and tested it against models with the following random effects added: (1) random intercept for dataset; (2) random intercept for individual hen; and (3) random intercepts for dataset and individual. We were not able to add random slopes due to sample size constraints. We selected the top model by minimizing AIC_c , thus restricting our scope of inference to the population level (Hebblewhite & Merrill, 2008; Vaida & Blanchard, 2005), which is appropriate given our research questions. We plotted the odds ratios of the fixed effects for each time period (*sjPlot*; Ludecke, 2023) and used these to interpret differences in sage-grouse habitat selection across temporal scales.

2.6 | Model validation

We validated our habitat selection models using standard methods (Boyce et al., 2002; Johnson et al., 2006; Morris et al., 2016). We compared binned predictions from the model (run on the training data) to predicted relative probability of selection (from running the model on the out-of-sample testing data) using *k*-fold validation and created predictive maps showing areas of higher selection (Boyce et al., 2002; Morris et al., 2016) (Appendix 1, Supporting Information S1).

3 | RESULTS

3.1 | Seasonal habitat selection analyses

The number of hens in the seasonal RSFs varied across seasons (nesting: $n = 447$ hens, brood-rearing: $n = 386$ hens, summer-fall: $n = 413$ hens, winter: $n = 385$ hens). Each seasonal model contained a different combination of fixed effects. The top models for nesting, brood-rearing, and summer-fall contained random intercepts for the individual and the dataset; the top model for winter included a random intercept for the dataset (Table 1). Coefficient estimates, standard errors, odds ratios, and *p*-values for the top RSF models are reported in Table 2; random effects are described in Appendix 2, Supporting Information S1.

Sage-grouse selection for topographical features and vegetation types varied seasonally (Figure 3). Across all seasons, hens selected higher shrub cover. Shrub selection was strongest during nesting (odds ratio [OR] = 2.01 [95% CI: 1.96–2.06]) and winter (OR = 2.14 [95% CI: 2.03–2.26]), but was still strong during brood-rearing (OR = 1.76 [95% CI: 1.71–1.80]) and summer-fall (OR = 1.74 [95% CI: 1.69–1.79]). Hens avoided higher tree cover across all seasons, especially during nesting (OR = 0.56 [95% CI: 0.51–0.61]) and brood-rearing (0.78 [95% CI: 0.73–0.83]). Hens slightly selected higher annual forb and grass cover during nesting (OR = 1.15 [95% CI: 1.12–1.18]) and brood-rearing (OR = 1.16 [95% CI: 1.13–1.20]), with the highest selection during summer-fall (OR = 1.23 [95% CI: 1.20–1.27]). Hens consistently avoided steeper slopes across all seasons (range: OR = 0.65 [95% CI: 0.62–0.68] [brood-rearing] to OR = 0.74 [95% CI: 0.72–0.76] [nesting] and OR = 0.74 [95% CI: 0.70–0.79] [winter]). They slightly selected bare ground during brood-rearing (OR = 1.09 [95% CI: 1.06–1.12]) and winter (OR = 1.12 [95% CI: 1.07–1.18]) and slightly avoided bare ground in summer-fall (OR = 0.92 [95% CI: 0.89–0.95]). They may have slightly avoided

TABLE 1 The set of candidate mixed-effects models compared at each temporal scale, each describing female greater sage-grouse habitat selection in central Montana at the relevant scale based on a resource selection function. The three mixed-effects model variants (random effects added for [a] dataset, [b] individual, or [c] dataset and individual) were added to the top fixed-effect model for each temporal scale. The top model for each time-period-specific set of candidate models is in bold. Vegetation cover variables (shrub, annual forbs, and grasses, or “annuals,” bare ground, tree, perennial forbs, and grasses, or “perennials,” and litter) are measures of percent cover at the 30 m² resolution. Grazing variables are categorical descriptors of the conservation-based grazing program (CGP). “DF” refers to degrees of freedom.

Time period	Fixed effects	Random effects	Delta-AICc	Residual DF
Nesting	Slope	Dataset	0.00	103,643
	Shrub	Individual		
	Annuals	Individual	3340.09	103,644
	Tree	Dataset	3731.25	103,644
	Pre-CGP			
Brood-rearing	Slope	Dataset	0.00	83,789
	Shrub	Individual		
	Bare ground	Individual	705.62	83,790
	Annuals	Dataset	2386.85	83,790
	Tree			
Summer–fall	Slope	Dataset	0.00	86,117
	Shrub	Individual		
	Bare ground	Individual	4553.23	86,118
	Annuals	Dataset	6029.73	86,118
	Tree			
Winter	Slope	Dataset	0.00	21,027
	Shrub	Individual	962.24	21,027
	Bare ground	Dataset	Did not converge	Did not converge
	Tree	Individual		
	Pre-CGP			
Annual	Slope	Dataset	0.00	294,442
	Shrub	Individual		
	Annuals	Individual	2021.2	294,442
	Tree	Dataset	18236.3	294,442
	Pre-CGP			

litter cover during summer–fall (OR = 0.98 [95% CI: 0.94–1.01]), but the effect was weak.

When compared to selection for non-CGP pastures (the reference category), sage-grouse hen selection for each CGP pasture type (Pre-, During-, and Post-CGP) varied seasonally. Hens selected Pre-CGP pastures (i.e., pastures where a CGP plan would later be implemented) over Non-CGP pastures during nesting (OR = 2.78 [95% CI: 2.53–3.06]), brood-rearing

(OR = 1.75 [95% CI: 1.55–1.98]), and winter (OR = 1.63 [95% CI: 1.27–2.07]). They slightly avoided Pre-CGP pastures compared to Non-CGP pastures during summer–fall (OR = 0.83 [95% CI: 0.68–0.99]). Hens selected pastures where CGP grazing plans were actively implemented (During-CGP) over Non-CGP pastures during nesting (OR = 1.31 [95% CI: 1.19–1.43]), brood-rearing (OR = 1.30 [95% CI: 1.18–1.43]), and winter (OR = 1.99 [95% CI: 1.67–2.37]), with no difference between During-

TABLE 2 Top models of greater sage-grouse hen habitat selection in central Montana for each temporal scale: Four seasons (nesting, brood-rearing, summer-fall, and winter), and the annual scale. Fixed effects are in plain text, and random effects are italicized. Covariates were centered and scaled. Coefficient estimates are presented from the top model of sage-grouse hen habitat selection. Odds ratios greater than 1 show positive selection (i.e., for every 1-unit increase in the variable, the selection increases by the proportion of the decimal, so an odds ratio of 1.23 indicates a 23% increase in relative probability of selection), whereas an odds ratio less than 1 indicates avoidance. Vegetation cover variables (shrub, annual forbs, and grasses, or “annuals,” bare ground, tree, perennial forbs and grasses, or “perennials,” and litter) are measures of percent cover at the 30 m² resolution. Grazing variables are categorical descriptors of the conservation-based grazing program (CGP). “SE” refers to standard error and “Sd” refers to standard deviation.

Temporal scale	Covariate	Coefficient	SE	Odds ratio	Pr(> z)	Sample sizes
Nesting	Intercept	−3.442	0.434	0.032	0.000	Hens: 447
	Slope	−0.304	0.016	0.738	0.000	Datasets: 4
	Shrub	0.697	0.013	2.008	0.000	Observations: 103,653
	Annuals	0.139	0.012	1.149	0.000	
	Tree	−0.581	0.046	0.559	0.000	
	Pre-CGP	1.023	0.049	2.782	0.000	
	During-CGP	0.267	0.045	1.306	0.000	
	Post-CGP	0.618	0.030	1.855	0.000	
	<i>Individual</i>	<i>Var: 0.940</i>	<i>Sd: 0.969</i>			
	<i>Dataset</i>	<i>Var: 0.744</i>	<i>Sd: 0.863</i>			
Brood-rearing	Intercept	−3.013	0.184	0.049	0.000	Hens: 386
	Slope	−0.428	0.019	0.652	0.000	Datasets: 4
	Shrub	0.564	0.014	1.757	0.000	Observations: 83,800
	Bare ground	0.087	0.014	1.091	0.000	
	Annuals	0.152	0.014	1.164	0.000	
	Tree	−0.246	0.034	0.782	0.000	
	Pre-CGP	0.560	0.063	1.751	0.000	
	During-CGP	0.262	0.048	1.300	0.000	
	Post-CGP	0.634	0.034	1.885	0.000	
	<i>Individual</i>	<i>Var: 0.724</i>	<i>Sd: 0.851</i>			
	<i>Dataset</i>	<i>Var: 0.126</i>	<i>Sd: 0.355</i>			
Summer-fall	Intercept	−4.538	1.283	0.011	0.000	Hens: 413
	Slope	−0.422	0.020	0.656	0.000	Datasets: 4
	Shrub	0.552	0.015	1.737	0.000	Observations: 86,129
	Bare ground	−0.084	0.017	0.919	0.000	
	Annuals	0.210	0.014	1.234	0.000	
	Tree	−0.131	0.027	0.877	0.000	
	Litter	−0.025	0.017	0.975	-	
	Pre-CGP	−0.192	0.095	0.825	0.05	
	During-CGP	0.008	0.065	1.008	-	
	Post-CGP	0.433	0.040	1.542	0.000	
	<i>Individual</i>	<i>Var: 1.195</i>	<i>Sd: 1.093</i>			
	<i>Dataset</i>	<i>Var: 7.191</i>	<i>Sd: 2.682</i>			
Winter	Intercept	−4.478	1.693	0.011	0.01	Hens: 385
	Slope	−0.296	0.033	0.744	0.000	Datasets: 3
	Shrub	0.761	0.028	2.140	0.000	Observations: 21,036
	Bare ground	0.115	0.026	1.122	0.000	
	Tree	−0.251	0.069	0.778	0.000	
	Pre-CGP	0.486	0.124	1.626	0.000	
	During-CGP	0.688	0.088	1.990	0.000	
	Post-CGP	0.794	0.069	2.212	0.000	
	<i>Dataset</i>	<i>Var: 8.538</i>	<i>Sd: 2.922</i>			
Year-long	Intercept	−3.291	0.169	0.037	0.000	Hens: 486
	Slope	−0.380	0.010	0.684	0.000	Datasets: 4
	Shrub	0.593	0.007	1.809	0.000	Observations: 294,451
	Annuals	0.151	0.007	1.163	0.000	
	Tree	−0.235	0.017	0.790	0.000	
	Pre-CGP	0.596	0.033	1.815	0.000	

TABLE 2 (Continued)

Temporal scale	Covariate	Coefficient	SE	Odds ratio	Pr(> z)	Sample sizes
	During-CGP	0.155	0.027	1.168	0.000	
	Post-CGP	0.489	0.018	1.631	0.000	
	Individual	Var: 1.599	Sd: 1.264			
	Dataset	Var: 0.100	Sd: 0.317			

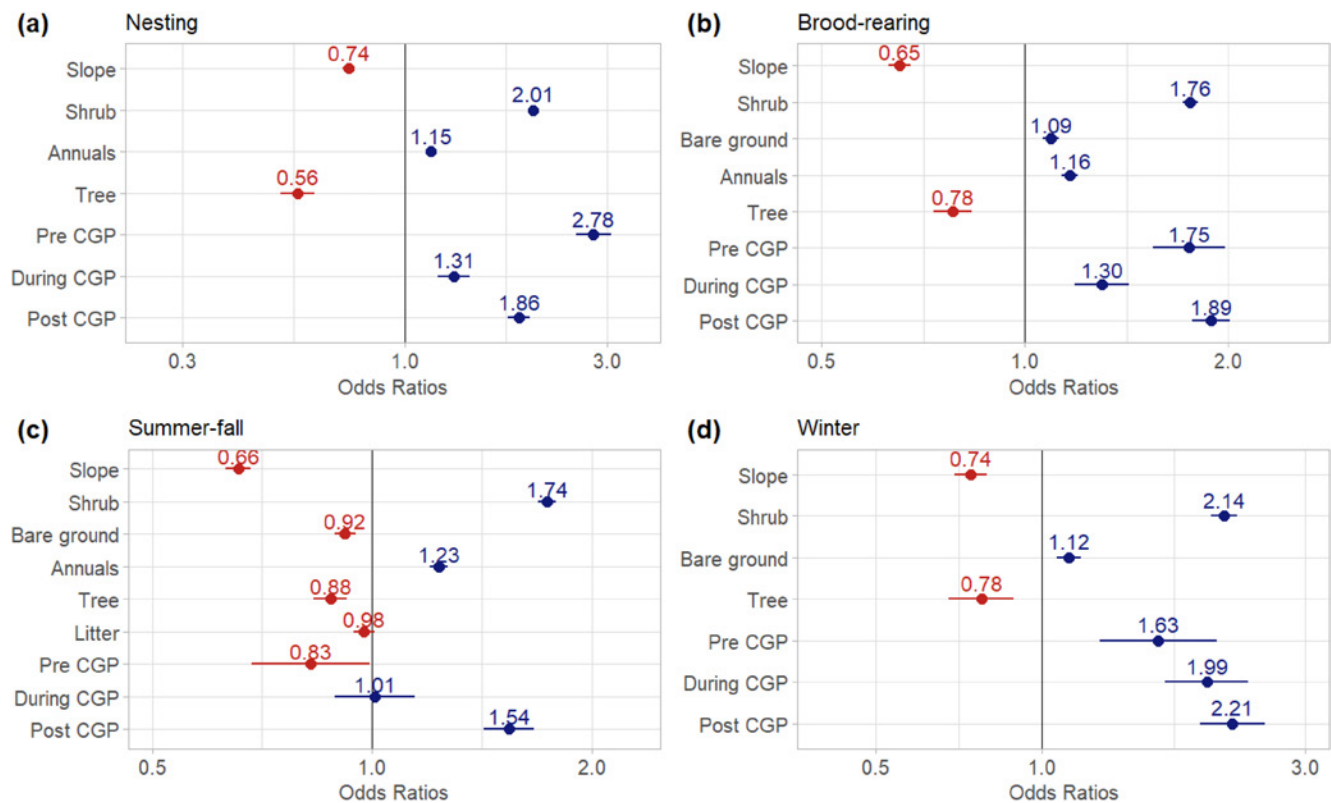


FIGURE 3 The odds ratios and 95% confidence intervals associated with the variables in the top models (resource selection functions) for the (a) nesting (April 1–May 31), (b) brood-rearing (June 1–July 15), (c) summer–fall (July 16–November 30), and (d) winter (December 1–March 31) seasons show seasonal patterns in greater sage-grouse hen habitat selection in central Montana. Odds ratios greater than 1 show positive selection (i.e., for every 1-unit increase in the variable, the selection increases by the proportion of the decimal, so an odds ratio of 1.23 indicates a 23% increase in relative probability of selection), whereas an odds ratio less than 1 indicates avoidance. An odds ratio of 2 indicates a 100% increase (i.e., a doubling) in the relative probability of selection. CGP refers to the “conservation-based grazing program”.

CGP and Non-CGP selection in summer–fall (OR = 1.01, [95% CI: 0.89–1.14]). Hens selected pastures where CGP grazing system implementation was complete (Post-CGP) over Non-CGP pastures during nesting (OR = 1.86 [95% CI: 1.75–1.97]), brood-rearing (OR = 1.89 [95% CI: 1.76–2.01]), summer–fall (OR = 1.54 [95% CI: 1.43–1.67]), and winter (OR = 2.21 [95% CI: 1.93–2.53]).

When habitat selection was compared among CGP categories (Pre-, During, and Post-CGP), patterns varied seasonally. During nesting, sage-grouse hens selected most strongly for Pre-CGP (OR = 2.78 [95% CI: 2.53–3.06]), followed by Post-CGP (OR = 1.86 [95% CI: 1.75–1.97]) and During-CGP (OR = 1.31 [95% CI: 1.19–1.43])

pastures. Notably, selection strength was lowest for During-CGP pastures, and after the CGP was complete (Post-CGP), selection strength was still lower than for Pre-CGP pastures.

During brood-rearing, hens selected most strongly for Post-CGP (OR = 1.89 [95% CI: 1.76–2.01]) and Pre-CGP (OR = 1.75 [95% CI: 1.55–1.98]) pastures (whose 95% CIs overlapped), followed by During-CGP (OR = 1.30 [95% CI: 1.18–1.43]) pastures. Although selection strength was lower for During-CGP pastures, after the CGP was complete (Post-CGP), selection returned to Pre-CGP levels.

During summer–fall, hens selected most strongly for Post-CGP (OR = 1.54 [95% CI: 1.43–1.67]) pastures. They

were neutral about During-CGP pastures (in comparison with Non-CGP pastures, OR = 1.01 [95% CI: 0.89–1.14]) and avoidant of Pre-CGP pastures (in comparison with Non-CGP pastures, OR = 0.83 [95% CI: 0.68–0.99]) whose CIs overlapped. During winter, the CIs for Post-CGP (OR = 2.21 [95% CI: 1.93–2.53]), During-CGP (OR = 1.99 [95% CI: 1.67–2.37]), and Pre-CGP (OR = 1.63 [95% CI: 1.27–2.07]) pastures all overlapped, implying similarly positive selection for all CGP pasture types.

3.2 | Annual habitat selection analysis

Hen habitat selection at the annual temporal scale was similar to the nesting and brood-rearing seasons (Figures 3 and S3b). Hens selected higher shrub (OR = 1.81 [95% CI: 1.78–1.84]) and annual forb and grass cover (OR = 1.16 [95% CI: 1.15–1.18]). They avoided tree cover (OR = 0.79 [95% CI: 0.76–0.82]) and steeper slopes (OR = 0.68 [95% CI: 0.67–0.70]). When compared to Non-CGP pastures, hens selected Pre-CGP (OR = 1.81 [95% CI: 1.70–1.94]), During-CGP (OR = 1.17 [95% CI: 1.11–1.23]), and Post-CGP (OR = 1.63 [95% CI: 1.57–1.69]) pastures. When selection was compared among CGP-enrolled pastures, hens selected most strongly for Pre-CGP (OR = 1.81 [95% CI: 1.70–1.94]), followed by Post-CGP (OR = 1.63 [95% CI: 1.57–1.69]) and During-CGP (OR = 1.17 [95% CI: 1.11–1.23]) pastures, although the CIs for Pre- and Post-CGP pastures nearly overlapped.

3.3 | Model validation

Predictive maps created as part of the model validation process show that hens selected similar areas across nesting, brood-rearing, and winter seasons (Figure 4) and the annual scale (Figure S3a). During nesting, brood-rearing, and winter, selected areas were most concentrated in the southern and central portions of the study area. Selected areas were more diffuse during the summer–fall season.

4 | DISCUSSION

4.1 | Landcover and topography selection

Sage-grouse hens selected a different combination of vegetation variables during each of the five time periods, but shrub cover was the strongest driver. Sage-grouse are a

sagebrush-obligate species, relying on sagebrush shrubs for food and cover throughout their annual cycle (Connelly et al., 2000); thus, given that sagebrush is the dominant shrub in this region, this finding corresponds with known life-history traits of sage-grouse. Assuming, therefore, that this selection for shrub cover is analogous to sagebrush cover, this selection for shrub cover aligns with current management strategies, which emphasize maintaining sagebrush cover for nesting habitat (Connelly et al., 2004). These results further contribute to the large body of evidence suggesting that sagebrush cover is important throughout the sage-grouse annual cycle (Braun et al., 2005; Connelly et al., 2000; Fedy et al., 2014; Smith et al., 2018b). However, we note that remotely sensed shrub cover layers may contain other shrub species that are less important to sage-grouse than sagebrush, and these results should not be construed to mean that any shrub will suffice for this sagebrush-obligate species.

During the nesting season, sage-grouse hens selected strongly for shrub cover, flatter slopes, and lower tree cover. This aligns with studies showing that hens select nest sites with greater sagebrush cover (Dinkins et al., 2016; Holloran et al., 2005; Smith et al., 2020) and fewer trees (e.g., avoid >3% conifer cover and dispersed trees, Severson et al., 2017). Sage-grouse also slightly selected annual forb and grass cover. This may provide protection from predators early in the nesting season (Coates & Delehanty, 2010; Watters et al., 2002), especially if it does not displace perennial forb and grass cover, which protects against predators as the nesting and brood-rearing seasons progress (Brussee et al., 2023). Given the dominance of perennial forb and grass cover across used points (40%–60%) compared to annual forb and grass cover (5%–20%) (derived from Allred et al., 2021), this link to annual cover may reflect selection for forbs that are associated with higher invertebrate biomass. We emphasize that this annual forb and grass cover layer likely includes native forb and grass species in addition to invasive annual forbs and grasses that are a concern across sage-grouse range. Hens typically avoid invasive annual grass cover during the nesting season (Lockyer et al., 2015) because it can decrease nest survival (Brussee et al., 2023).

Hen habitat selection during brood-rearing was similar to the nesting season with strong selection for shrub cover, flatter slopes, and lower tree cover. Sage-grouse also slightly selected for annual forb and grass cover and bare ground. The mechanism driving selection for higher shrub and annual cover likely aligns with the nesting season. Hens must manage predation risk to their broods during this season, thus requiring ample vegetative cover (Connelly et al., 2004). As they raise their broods, they

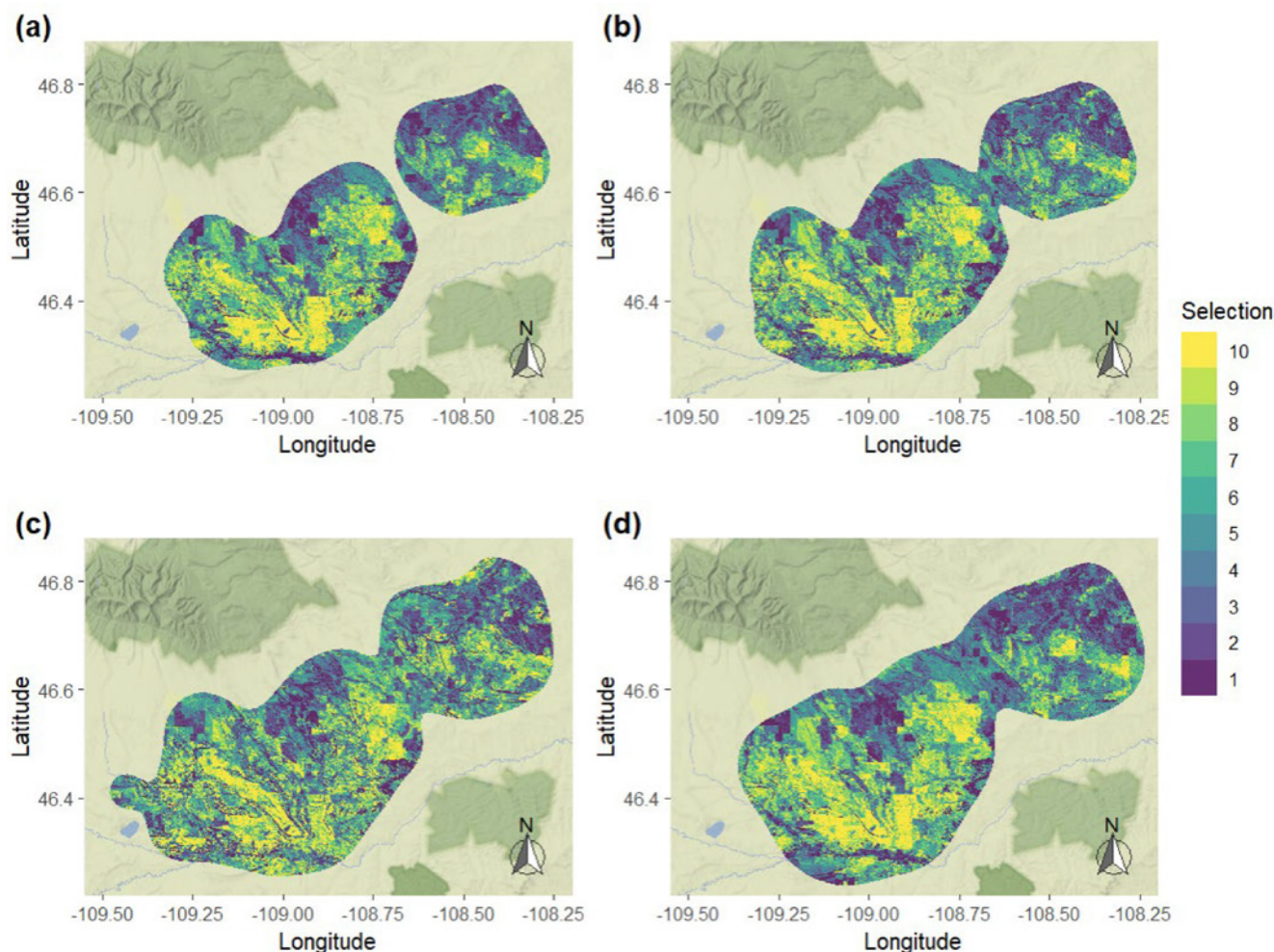


FIGURE 4 Predictive maps show the relative probability of habitat selection by greater sage-grouse hens during each of the four seasons—(a) nesting (April 1–May 31), (b) brood-rearing (June 1–July 15), (c) summer–fall (July 16–November 30), (d) and winter (December 1–March 31)—averaged across the study duration (2011–2019). The predicted relative probability of use for each season was derived from the seasonal fixed effects model, cropped to the 95% kernel density estimate for that season, and validated (Boyce et al., 2002). Relative probability of selection was scaled to 10 equal-area bins with the highest relative probability of selection represented as 10 and the lowest relative probability of selection represented as 1 (Boyce et al., 2002; Morris et al., 2016).

must manage trade-offs between predation risk and resource access (Cresswell, 2008; Dinkins et al., 2012), even selecting areas that are riskier brood-rearing habitats periodically (Aldridge & Boyce, 2007). Selection for lower elevations may be correlated with mesic areas, which hens select during brood-rearing (Atamian et al., 2010; Fischer et al., 1996) to access arthropods and forbs (Schreiber et al., 2015). In this part of sage-grouse range, most mesic areas are found in lower-elevation depressions such as wet meadows (Donnelly et al., 2018). We suggest that future studies assess whether hens select covariates associated with mesic resources, like soil moisture and normalized difference vegetation index (a measure of vegetation “greenness”), to better understand potential trade-offs between predation risk and food resource access.

During the summer–fall season, sage-grouse selected shrub cover, annual forb and grass cover, and flatter slopes. They avoided bare ground and weakly avoided litter cover. Selection for shrub cover was slightly lower than during nesting and winter, likely because sage-grouse use alternative food sources during this season. Avoidance of bare ground during summer–fall may result from seeking thermal cover during hot and dry weather.

During the winter, sage-grouse strongly selected shrub cover, lower tree cover, and flatter slopes. They slightly selected areas with more bare ground. Selection for high shrub cover during this season aligns with most winter habitat selection studies (Wallestad & Pyrah, 1974), given that sage-grouse use sagebrush for both food and cover (Connelly et al., 2000). This is plausible if the shrub cover derived from remotely sensed layers

is available above the snow. We suggest that future work continues to investigate habitat selection in the context of winter weather conditions, especially extreme winter weather events, as they can affect hen survival (Moynahan et al., 2006).

At the annual temporal scale, sage-grouse hens selected shrub cover, flatter slopes, lower tree cover, and slightly higher annual forb and grass cover. Overall, the patterns of habitat selection we observed align with patterns documented in other parts of their range despite the differences in types of sagebrush, vegetation, moisture and temperature patterns, and topography reflected in the seven sage-grouse management zones (Stiver et al., 2006). We expected that selection patterns might differ in the cooler and wetter climate in central Montana (Pyke et al., 2015) than in hotter, drier areas in the Great Basin, but this was not the case.

It is worth noting that these results are based on data sampled unevenly across seasons, meaning that models for some seasons (e.g., nesting and brood-rearing) were based on larger sample sizes than others (e.g., winter). These discrepancies could lead to an underrepresentation of habitat selection patterns during the seasons with smaller sample sizes. Additionally, the error rate associated with the aerial survey method that dominated summer-fall and winter sampling is higher than the rate associated with survey methods in other seasons. As such, we suggest interpreting results from the summer-fall and winter seasons with caution, as the higher error rate of aerial locations could limit the ability to ascertain covariate relationships. Last, the GPS-based hen locations recorded in 2019 may be biased toward resting locations based on the time of day that they were recorded (Supporting information S1). Although these locations were a large proportion of the 2019 data, they only made up a small fraction of the whole dataset (Table S1).

4.2 | Grazing program-related selection: CGP versus non-CGP pastures

Across all time periods except for summer-fall, sage-grouse hens strongly selected CGP pastures (i.e., Pre-, During-, and Post-CGP pastures) in comparison with Non-CGP pastures. One possible reason for this difference is that grazing pressure and duration followed different patterns in CGP vs. Non-CGP pastures. Based on the 32% of pastures for which used Animal Unit Months, or “used AUMs” (a rough estimate of forage consumed by livestock, details in Appendix 1, Supporting Information S1, Figure S4, Table S3) data were available, the distribution of used AUMs was far more right-skewed

in Non-CGP pastures than in CGP pastures, even though the median value was similar across CGP and Non-CGP pastures. Based on the 30% of pastures with grazing duration information (Appendix 1, Supporting Information S1, Table S3), grazing durations tended to be longer and more variable in Non-CGP pastures than in CGP pastures, where durations were more similarly distributed (Figure S4, Table S3).

However, it is worth noting that pasture area was also right-skewed and more variable in Non-CGP pastures (Figure S4, Table S3), likely due in part to the fact that rotational grazing systems such as those implemented during the CGP often use smaller areas to rotate livestock through pastures. As such, the larger pasture areas in the Non-CGP systems can likely support longer grazing durations and higher used AUMs, even as light to moderate grazing intensity in these pastures may lead to increased pasture spatial heterogeneity as livestock preferentially graze higher-quality forage (Nunes et al., 2019). Additionally, Non-CGP pastures are a mixture of public and private land, whereas CGP pastures are exclusively located on private land where land owners voluntarily agreed to participate in the CGP. Differences in the way that public lands are grazed (including turnout dates, duration, and intensity) may contribute to differences in underlying range quality that were not measured as part of this study.

4.3 | Grazing program-related selection compared among CGP pastures (Pre-, During-, and Post-CGP)

Sage-grouse strongly selected Pre-CGP pastures at both the seasonal and annual temporal scales except for summer-fall when they slightly avoided them. During the nesting season, sage-grouse were 178% more likely to choose a Pre-CGP pasture than a Non-CGP pasture, indicating that they selected these pastures even before CGP rotational grazing systems were implemented. To understand this result, it is helpful to note that the pastures enrolled in the CGP were already hypothesized to be high-quality sage-grouse habitat based on their presence within state-designated core areas. These are predicted to help maintain sage-grouse populations (Gamo & Beck, 2017) and avert population losses over the long term (Copeland et al., 2013) in concert with other conservation strategies. However, much of the study area outside of CGP pastures is also within these core areas, which indicates that there may be some unmeasured difference between CGP and Non-CGP pastures. Our ancillary grazing metrics (Appendix 1, Supporting Information S1, Figures S2 and S4, Table S3) do not indicate any major

differences between Pre-, During-, and Post-CGP pastures. However, it is possible that unmeasured differences in range quality between the privately owned CGP pastures and the mixture of public and privately owned pastures made Pre-CGP pastures more appealing to sage-grouse even prior to changing the grazing system, with the exception of the summer–fall season.

During active implementation of 3-year CGP grazing regimes (During-CGP), nesting and brood-rearing sage-grouse did not select these pastures as strongly as they did either before (Pre-CGP) or after (Post-CGP) grazing system implementation. In our study area, CGP grazing plans limited offtake to <50% of the current year's key livestock forage species growth and limited grazing duration to 45 days at a time (NRCS, 2017) within the 3-year contract period (During-CGP). However, guidelines do not specify the seasonal timing of 45-day rotations, outside of the requirement to shift timing each year. Not knowing the specific time that each 45-day rotation occurred limited our ability to identify the mechanism behind lower selection for During-CGP than Pre- and Post-CGP pastures during nesting and brood-rearing. However, it is possible that this shift in habitat selection is due to a relationship between vegetation productivity and grazing timing. A large-scale study of grazing, vegetation productivity, and sage-grouse population growth across Wyoming found that underlying vegetation productivity intersected with the timing and intensity of grazing to mediate grazing effects on sage-grouse populations (Monroe et al., 2017). Similarly, it is plausible that grazing during the nesting and brood-rearing season intersected with vegetation productivity such that the grass cover available for nesting and brood-rearing decreased, causing hens to move to other pastures with potential implications for reproductive rates, although a recent study found that vegetation productivity in this study area was more closely tied to environmental factors than grazing (Reintsma et al., 2024). We suggest that future studies of the effect of grazing programs on sage-grouse habitat selection explicitly consider the timing of grazing in relation to the timing of forage growth (i.e., productivity).

After CGP grazing systems were complete (Post-CGP), sage-grouse selection for these pastures varied by season. Most strikingly, sage-grouse strongly selected Post-CGP pastures during the summer–fall, whereas prior to CGP grazing system implementation (Pre-CGP), they strongly avoided these pastures, even in comparison with Non-CGP pastures. Additionally, during this season, selection strength consistently increased from Pre-CGP to During-CGP to Post-CGP pastures. Although the mechanism for this shift is uncertain, it is possible that the CGP grazing plans may have changed

the vegetation structure within these pastures to be more favorable for sage-grouse hens over time. Grazing can stimulate plant growth in some contexts, depending on the timing and intensity, and sage-grouse prefer areas with more new growth (Belsky, 1987; Georgiadis et al., 1989; Li et al., 2021). During the summer–fall in particular, it seems plausible that this could have resulted from differences in livestock turnout timing. Livestock turnout dates (albeit only available for 30% of all pastures) on CGP pastures (Pre-, During-, and Post-CGP) disproportionately occurred during the brood-rearing and summer–fall seasons (Figure S2). In contrast, turnout dates on Non-CGP pastures occurred most frequently during nesting. These differences in turnout timing may have resulted in vegetation conditions that sage-grouse increasingly selected over time.

Ultimately, in the absence of an experimental design that randomly placed CGP pastures on the landscape, and without more information about the mechanisms driving sage-grouse habitat selection, it is difficult to determine whether the CGP benefited this sage-grouse population. In general, sage-grouse hens selected CGP pastures over non-CGP pastures (except for summer–fall), but during the summer–fall, sage-grouse consistently increased their selection from Pre-CGP to During-CGP to Post-CGP pastures. However, the nesting, brood-rearing, and annual models all showed lower selection for During-CGP pastures than Pre- or Post-CGP pastures, suggesting that the three-year contracts may not be beneficial for sage-grouse during key reproductive seasons. Overall, it is important to weigh these trade-offs as managers consider how to proceed with implementing grazing systems for sage-grouse conservation.

5 | CONCLUSIONS

We identified vegetation, topography, and grazing system characteristics that sage-grouse hens select at seasonal and annual temporal scales. Higher shrub cover, lower tree cover, and flatter slopes were strong habitat selection drivers across all time periods. This suggests that maintaining sagebrush shrublands and areas of lower tree cover is important for conservation initiatives targeting sage-grouse. We also found that across all time periods except for summer–fall, sage-grouse hens strongly selected CGP pastures (i.e., Pre-, During-, and Post-CGP pastures) in comparison with Non-CGP pastures. They most strongly selected pastures where CGP grazing systems were complete (Post-CGP) during the summer–fall. However, it is important to note that sage-grouse were selecting pastures enrolled in the CGP even before the CGP rotational grazing systems were implemented. This

raises the question of whether CGP pasture enrollment patterns and unmeasured, underlying differences between Non-CGP and CGP pastures are driving these results. Further research is needed to tease apart these factors from grazing system differences before concluding whether the CGP benefited sage-grouse habitat selection.

AUTHOR CONTRIBUTIONS

JEH led the analysis and writing. EGS and SPC supported the writing and revision. LIB and MS led the fieldwork and contributed to the writing and revision. VJD provided project oversight and contributed to the writing and revision.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

Data can be obtained from Montana Fish, Wildlife, and Parks by submitting an information request.

ORCID

Jennifer E. Helm  <https://orcid.org/0000-0002-7205-4812>

Elizabeth G. Simpson  <https://orcid.org/0000-0002-6107-0286>

Victoria J. Dreitz  <https://orcid.org/0000-0002-9383-2329>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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