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ORIGINAL PAPER

Novel environmental variables help explain winter weather effects on activity and habitat selection of greater sage-grouse along the border of Colorado and Wyoming, USA

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Abstract

For non-hibernating species within temperate climates, survival during severe winter weather often depends on individuals' behavioral response and available refugia. Identifying refugia habitat that sustains populations during adverse winter conditions can be difficult and complex. This study provides an example of how modeled, biologically relevant snow and weather information can help identify important relationships between habitat selection and dynamic winter landscapes using greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") as a model species. We evaluated whether sage-grouse responded to weather conditions in two ways: through (1) positive selection for refugia habitat to minimize adverse weather exposure, or (2) lowered activity level to minimize thermoregulation and locomotion expense. Our results suggested that sage-grouse respond to winter weather conditions by seeking refugia rather than changing daily activity levels. During periods of lower wind chill temperatures and greater wind speeds, sage-grouse selected areas with sheltered aspects and greater sagebrush (*Artemisia* spp.) cover. Broadly, sage-grouse selected winter home ranges in sagebrush shrublands characterized by higher wind chill temperatures, greater wind speeds, and greater blizzarding conditions. However, *within* these home ranges, sage-grouse specifically selected habitats with greater above-snow sagebrush cover, lower wind speeds, and lower blizzarding conditions. Our study underscores the importance of examining habitat selection at narrower temporal scales than entire seasons and demonstrates the value of incorporating targeted weather variables that wholistically synthesize winter conditions. This research allows identification of refugia habitat that sustain populations during winter disproportionate to their spatial extent or frequency of use, facilitating more targeted management and conservation efforts.

Keywords Centrocercus urophasianus · Refugia habitat · Resource selection function · Snow · SnowModel · Wind chill temperature

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Introduction

Winter in temperate zones is often a time of greatest energetic demand for vertebrate species (Martinka 1967; Gray and Prince 1988). Within winter, severe weather events, often measured by large swings above or below long-term averages in meteorological variables such as temperature, wind speed, or precipitation, can impact population vital rates and have carry-over effects on individual fitness in subsequent seasons (Altwegg et al. 2006; Harrison et al. 2011; Williams et al. 2014; Giraudoux et al. 2019; Londe et al. 2021). The combination of severe weather and accumulating snow can create ecological bottlenecks for populations that must concentrate on spatially restricted patches of remaining food and cover (Barrett 1982; Payne 1999; Morrison et al. 2003; Coulson et al. 2001). The severity of these bottlenecks often depends on the availability of refugia, defined as sites that biota will retreat to, or persist in, to resist periods of adverse environmental conditions (Samways 1990; Keppel et al. 2012; Shipley et al. 2020).

During temperate-zone winters, extreme shifts in snow and other weather conditions can impact organisms by increasing thermoregulation costs (Merritt 1995; Gilbert et al. 2008; Shipley et al. 2021), obstructing movements and behaviors (Stien et al. 2010; Richard et al. 2014; Butler et al. 2019; Pedersen et al. 2021; Sheppard et al. 2021), and lowering forage availability or increasing foraging effort (Sonerud 1986; Dumont et al. 2005; Visscher et al. 2006). Effective evaluation of relationships between animal behavior and winter conditions has historically been hampered by a lack of technical expertise and technology capable of capturing the complex and dynamic nature of snow and weather at ecologically relevant spatiotemporal scales (Reinking et al. 2022). Snow and weather observations are often limited to a few point measurements (e.g., air temperature and snow depth; Leckenby and Adams 1986; Lishawa et al. 2007). Sophisticated numerical modeling tools can simulate snow and other weather information that varies across space and time at wildlife-relevant scales to fill gaps in observational datasets; moreover, these systems can incorporate available field and remote sensing observations within a data-model fusion framework to bring model results closer to reality (Glass et al. 2021; Liston et al. 2020; Pedersen et al. 2021; Reinking et al. 2022). These models can also combine weather information into synthetic variables that create a clearer, more nuanced, picture of the environmental conditions that wildlife experience.

We used greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse) as a model species to illustrate how simulated, biologically relevant weather information can identify important relationships between winter environmental variables and wildlife behavior that would remain poorly understood without this interdisciplinary approach (Reinking et al. 2022). Grouse (*Tetraonini*) have both physical (e.g., feathered tarsi and nares) and behavioral (e.g., snow burrowing) cold-climate adaptations that make them especially suited to winters in higher latitudes of the Northern Hemisphere. These adaptations make them unique among Galliformes so that winter is generally not viewed as the most difficult season, unlike many other wildlife species in the temperate and frigid climate zones. Sage-grouse show high fidelity to the winter ranges they select, which contain mix-gender flocks of 5 to several hundred individuals (Beck 1977; Smith et al. 2019; Schroeder et al. 2020) and may overlap with or be separate from their breeding ranges (10 to greater than 200 km apart; Newton et al. 2017; Pratt et al. 2019). Outside of two in-lab, sage-grouse thermoregulation studies (Sherfy and Pekins 1994, 1995), the effects of weather and snow on the behavior of sage-grouse have been largely speculative (e.g., Anthony and Willis 2010; Dzialak et al. 2013). If severe weather events are infrequent or study periods are mild, then randomly selecting sage-grouse locations across a winter season for purposes of modeling resource selection might fail to detect the acute impacts of severe weather on sage-grouse behavior. Failure to account for temporary, but important, selection of refugia from severe weather could result in potentially false conclusions that winter weather has no effect on sage-grouse beyond snow mediating available sagebrush (*Artemisia* spp;) used for cover and forage (Call and Maser 1985; Connelly et al. 2000; Zablan 2003). Lower survival rates have been documented following prolonged periods of severe weather (as low as 67% compared to 98% survival during milder years; Moynahan et al. 2006; Anthony and Willis 2010). Sage-grouse entering the breeding season with lower body condition have reduced reproductive ability (Beck and Braun 1978; Vehrencamp et al. 1989), indicating there are energetic costs associated with surviving severe winters. Therefore, it is possible that refugia from harsh winter weather confers fitness benefits for sage-grouse during the winter season and beyond. Understanding the relationship between sage-grouse habitat selection and behavior, as influenced by winter weather conditions, may facilitate the identification of specific characteristics of refugia that buffer survival for sage-grouse during severe winters.

Our objectives aimed to evaluate whether sage-grouse responded to winter weather in two possible ways: (1) through positive selection for refugia habitat to minimize exposure to severe winter weather, or (2) through lowered activity level. For our first objective (refugia habitat selection), we tested observations and predictions made by experts in the field regarding sage-grouse winter habitat response to weather conditions. We compared two hypotheses to assess whether sage-grouse habitat selection within winter ranges was affected by weather. Hypothesis 1, Winter Landscape hypothesis: shrub availability relative to snow depth alone is the primary driver of winter habitat selection, as suggested by Call and Maser (1985) and others (Hupp and Braun 1989; Connelly et al. 2000; Crawford et al. 2004). Hypothesis 2, Winter Weather hypothesis: weather conditions affect the way sage-grouse select or interact with habitat features, as suggested by Dzialak et al. (2013) and Anthony and Willis (2010).

We predicted that snow conditions would affect habitat selection, even if other weather conditions did not play a role. Therefore, support for Hypothesis 1 (Winter Landscape hypothesis) would indicate that daily weather played no role in winter habitat selection, while support for

Hypothesis 2 (Winter Weather hypothesis) would indicate that sage-grouse altered habitat selection to seek refugia depending on prevailing weather conditions. In building our habitat selection models, we considered several predicted responses associated with how snow and weather conditions interact with terrain and vegetation characteristics. These expected predictions came from observations in the literature and personal observations in the field and are described in Table 1.

Sage-grouse may change their behavior in response to weather conditions even if weather is not predictive of habitat selection. Therefore, for our activity response objective, we asked whether sage-grouse altered their activity levels in response to daily weather conditions. We quantified daily sage-grouse activity (DSA) from a synthesis variable that accounted for several movement parameters, including distance between subsequent locations and acceleration metrics. In turn, we used DSA to index when grouse were conserving metabolic reserves and minimizing thermogenic outputs. To explain daily activity levels, we compared a baseline Landscape-Only model of landscape predictors (topography and vegetation) against two environmental predictions: (1) snow depth influenced grouse daily activity levels relative to other landscape features; and (2) weather conditions influenced activity levels depending on the refugia provided by occupied habitat characteristics (topography, vegetation, and snow depths). Support for prediction 1 over the base model would suggest that shifting snow depths influenced the way the landscape influenced sage-grouse behavior. Support for prediction 2 over prediction 1 would suggest that sage-grouse also altered activity levels in response to weather conditions, depending on whether the occupied areas provided shelter. We predicted that sage-grouse activity would decrease during harsh winter days while they sought shelter in areas with greater shrub cover or opportunity to snow burrow (Back et al. 1987).

Our research provides new insights into the behavioral adaptations and refugia habitat that enable sage-grouse and other vertebrates to withstand adverse winter conditions. This work also provides information on how synthesized weather variables add value to habitat studies by incorporating weather information in ways that are more relevant to wildlife. This is a relatively new technique that may help researchers better quantify weather conditions that are important in their wildlife applications (Glass et al. 2021; Reinking et al. 2022).

Study area

Our study area included portions of southern Sweetwater and Carbon counties, Wyoming, and northern Moffat County, Colorado. The study area, as defined by the extent of movement of the GPS-fitted grouse, encompassed 9,687 km^2, comprised of BLM-managed (73%), private (24%), and Wyoming state (3%) land. Sage-grouse winter ranges occurred in areas categorized as cold arid-steppe (Kottek et al. 2006). Elevation within the study area ranged from 1,600 to 3,300 m (USGS 2016) and annual precipitation ranged from 20 to 63 cm (PRISM Climate Group 2022). Dominant shrubs included Wyoming big sagebrush (*A. tridentata wyomingensis*), saltbushes (*Atriplex spp.*), greasewood (*Sarcobatus vermiculatus*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Shrub assemblies occurred across a gradient of precipitation amounts and soil types; they were dominated by sandy loams, but also included sand dunes and alkali complexes (Soil Survey Staff 2015). We obtained sage-grouse location data across winters 2018/2019 and

Table 1 Predictions for interactions between weather or snow conditions on greater sage-grouse selection for landscape characteristics. We developed predictions based on published findings in the literature and through field observations in our study area

Interaction	Predictions	Sources
Snow		
Snow × Sagebrush height	Select higher sagebrush height when exposed vegetation is low and lower sagebrush height when exposed vegetation is high	Hagen et al. 2011, Dzialak et al. 2013; Smith et al. 2016, 2014
Snow × TPI[a]	Select ridges when exposed sagebrush is high and drainages when exposed sagebrush is low	Schoenberg 1982, Remington and Braun 1985, Hupp and Braun 1989
Weather		
Wind chill temperature × HLI[b]	Select warmer aspects during low temperatures	Sherfy and Pekins 1995
Wind chill temperature × Sagebrush canopy cover	Select greater sagebrush cover during low temperatures	Swanson et al. 2013, Dzialak et al. 2013
Wind speed × Sagebrush canopy cover	Select shelter in greater cover during high-wind periods	Hupp and Braun 1989; Sherfy and Pekins 1995
Wind speed × TPI[a]	Select shelter in drainages (TPI < 0) during high-wind periods	Sherfy and Pekins 1995

[a]Terrain position index

[b]Heat load index

2019/2020. Average winter (1 Dec–14 Mar) temperatures fell within the 29th (-6.4 °C) and 31st (-6.6 °C) percentiles and total winter precipitation fell within the 63rd (24 cm) and 91st (30 cm) percentiles, respectively, compared with winters during the previous 30 years (1988–2022) in our study area (PRISM 2022).

Materials and methods

Capture and monitoring

We captured and radio-marked adult female sage-grouse using spotlight and hoop-net methods (Giesen et al. 1982; Wakkinen et al. 1992) around leks during spring or near roost sites of previously-marked grouse during summer and winter. We fitted female sage-grouse with rump-mounted GPS transmitters (GPS PTT [GeoTrak, King George, Virginia, USA], ~37 g total weight; or e-obs Bird Solar [e-obs GmbH, Grunwald, Germany], ~30 g total weight). GeoTrak transmitters uploaded GPS locations to satellites used by the Argos system (Woods Hole Group, Largo, Maryland, USA) every 3 days, and were programmed to acquire 4 locations per day from 1 November through 14 March (at 0000, 0900, 1200, and 1500 h MST). We programmed e-obs transmitters to collect one location every 10 min (from 0200 to 2200 h MST) and stored locations onboard to be downloaded manually in the field or by fixed-wing aircraft. Incorporated in each e-obs transmitter was an accelerometer that measured the acceleration (G) of each grouse relative to Earth's gravitational acceleration. During each location acquisition, the accelerometer measured G along the x, y, and z planes over 5 s. We downloaded data from the e-obs transmitters approximately every 3 months during fall/winter. After mortality events, we redeployed recovered transmitters during the following spring or winter. All sage-grouse capture, handling, and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols 20170324AP00266-01) and Wyoming Game and Fish Department Chap. 33-1160 permit.

Landscape and weather variables

We explored predictor variables that described topography, vegetation, snow, and weather for both our resource selection and behavioral models (Table 2). We calculated a heat load index, which is a measure of solar radiation; it is used to estimate the air temperature potential of an area and identify places that are hotter and drier compared to those that are cooler and wetter (0–1, with 1 indicating hot and dry; McCune and Keon 2002; Geomorphometry and Gradient Metrics; Evans et al. 2014). We used a 30-m digital elevation model (U.S. Geological Survey 2011) to calculate Terrain Ruggedness Index (Wilson et al. 2007) and Terrain Position Index (Weiss 2001). We used 30-m resolution sagebrush and shrub fractional component and height datasets from the National Land Cover Database (Xian et al. 2015; Dewitz 2021). We calculated the proportion of juniper (*Juniperus* spp.)-dominated landscapes (hereafter "juniper") from the LANDFIRE Existing Vegetation Type raster dataset (LANDFIRE 2016). Juniper was restricted to Colorado Plateau pinyon (*Pinus edulis*)-juniper woodland and Rocky Mountain foothill limber pine (*P. flexilis*)-juniper woodlands (LANDFIRE 2016).

We defined our winter season to be 1 December–14 March. We considered these dates the core winter period, when all sage-grouse were expected to be on winter range and severe weather events were most likely to occur. We confirmed that all individuals were occupying winter ranges during these dates using the seasonal delineation methodology described in Pratt et al. 2017. The median dates of arrival to, and departure from, winter range were10 November and 20 March, respectively. (Smith et al. 2021).

We generated weather and snow variables for winters 2018/2019 and 2019/2020 using MicroMet and SnowModel (Liston and Elder 2006a, b; and Appendices in Liston et al. 2020). MicroMet and SnowModel are detailed numerical process models that produce weather, snow, and other environmental variables that evolve realistically across space and through time. MicroMet spatially downscales basic meteorological information including air temperature, precipitation, relative humidity, wind speed, and wind direction (Liston and Elder 2006a). Using this downscaled meteorological forcing, SnowModel simulates the interactions between weather and landscape characteristics to produce realistic snow and environmental information at wildlife-relevant spatiotemporal scales (Liston and Elder 2006b; and Appendices in Liston et al. 2020; Reinking et al. 2022). Meteorological inputs used to drive MicroMet and SnowModel consisted of North American Land Data Assimilation System, Version 2 (NLDAS-2) forcing data (Cosgrove et al. 2003). Landscape inputs included topography (United States Geological Survey [USGS] 3D Elevation Program Digital Elevation Model; Stoker and Miller 2022) and land cover type (North American Land Change Monitoring System [NALCMS] 30-m, 2015 land cover; Commission for Environmental Cooperation 2015). Our land cover datasets also integrated 270 field observations of vegetation height across our study area to ensure the snow holding depths used in SnowModel were congruent with field observations. SnowModel produced spatially explicit distributions of weather and snow variables at daily temporal resolution and 30-m × 30-m spatial resolution. SnowModel variables (Table 2) included mean air temperature (°C); mean wind

Table 2 Variables used in models evaluating greater sage-grouse winter habitat selection and daily activity, with literature sources for variables that have been predictive of sage-grouse winter habitat selection or survival

Variable name	Description	Predicted selection response	Literature
Topographic			
Heat Load Index (HLI)	HLI approximates an index of coolest to warmest aspects (0–1; McCune and Keon 2002)	Positive or negative	Hupp and Braun 1989, Dzialak et al. 2013, Smith et al. 2021
Terrain Position Index (TPI)	Difference between location and mean elevation of surrounding 8 cells. TPI > 0 indicates terrain position above mean elevation.	Positive	Hupp and Braun 1989; Coates et al. 2016,
Terrain Roughness Index (TRI)	Terrain relief (Wilson et al. 2007)	Negative	Doherty et al. 2008; Coates et al. 2016, Hagen et al. 2011
Vegetation			
Juniper land cover (Juniper)	Proportion of juniper land cover (LANDFIRE 2016)	Negative	Coates et al. 2020, Smith et al. 2021
Sagebrush canopy cover (Sage)	Percent canopy cover of big sagebrush	Positive	Doherty et al. 2008; Hansen et al. 2016, Smith et al. 2021
Shrub canopy cover (Shrub)	Percent canopy cover of all shrub species	Positive	Hagen et al. 2011
Sagebrush height (Sageht)	Mean height (cm) of sagebrush	Positive	Dzialak et al. 2013, Smith et al. 2021
Shrub height (Shrubht)	Mean height (cm) of all shrub species	Positive or negative	Dzialak et al. 2013, Smith et al. 2016, Coates et al. 2020
Protruding vegetation height (Prot)	Height (cm) of vegetation protruding above snow	Positive	Smith et al. 2021
Weather			
Vegetation above snow depth (Bnry)	A binary variable representing whether the vegetation protrudes above the snow	Positive	Hupp and Braun 1989
Blizzard (Bliz)	Daily mean of mass of snow blowing in the air and at ground level (kg/m/s)		–
Air temperature (Tair)	Mean daily air temperature (degrees Celsius)	Positive	Moynahan et al. 2006; Anthony and Willis 2010; Dinkins et al. 2017
Wind chill temperature (Chil)	Mean daily wind chill temperature (°C) meant to convey how cold it feels, based on air temperature (Tair) and wind speed (Wspd)	Positive	Sherfy and Pekins 1995; Moynahan et al. 2006; Anthony and Willis 2010
3-day trend in wind chill temperature (Chil.trend)[a]	Slope of the line for wind chill temperature values between 3 previous days		–
Wind speed (Wspd)	Daily mean wind speed (m/s)	Negative	Sherfy and Pekins 1995
Snow depth (Snod)	Daily snow depth (cm)	Positive or negative	Moynahan et al. 2006; Anthony and Willis 2010

[a]Parameter included only in sage-grouse activity model

chill temperature (i.e., an index of the cold a person feels with zero warming from solar radiation;°C); mean wind speed (m/s); snow depth (cm); whether vegetation protruded above snow (binary, 1 = vegetation protruded above snow level, 0 = vegetation did not protrude); and height of vegetation protruding above the snow (cm).

We developed a ground-blizzard variable (i.e., blizzarding) to quantify the impact of winter snowstorm and blowing snow blizzard conditions on animal behavior. We assumed two different conditions could produce near-surface blowing snow associated with blizzarding: (1) precipitating snow particles (i.e., snowfall) that are blown horizontal by the wind, and (2) surface snowpack particles that are picked up and blown by the wind. This blizzard variable, *B*, has units of kg m^{-1} s^{-1}, and represents the mass of snow blowing in the air at ground level per unit width per unit time,

$$B = P + S \tag{1}$$

where *P* (kg m^{-1} s^{-1}) is the precipitation contribution, and *S* (kg m^{-1} s^{-1}) is the surface snowpack contribution, to blizzarding.

The snow precipitation blowing in the air, or the snowfall contribution to blizzarding is given by,

$$P = \rho_w \, P_s \, W \tag{2}$$

where P_s (m) is the daily total snowfall, W (m s^{-1}) is the daily average wind speed, and ρ_s is the water density (1000 kg m^{-3}). This equation turns precipitating snow into a horizontal mass flux moving at the wind speed, W.

Snow particles can also be removed from the snow surface by the wind and transported near the surface by the processes of saltation and suspension (e.g., Tabler 2003). This surface snow contribution, S, is defined using the saltation, Q_s (kg m^{-1} s^{-1}) and suspension Q_t (kg m^{-1} s^{-1}) fluxes calculated by the SnowTran-3D blowing snow model (Liston and Sturm 1998; Liston et al. 2007),

$$S = Q_s + Q_t \quad (3)$$

See Liston and Sturm (1998) for a detailed description of the Q_s and Q_t formulations. In general, non-zero S values require (1) the wind speeds to be $W > 5$ m s^{-1} (below this value the snow does not move in response to the wind), and (2) the snow to be deeper than the vegetation height (or vegetation snow holding depth; see Liston and Sturm 1998; Liston and Hiemstra 2011).

Another synthesis variable used in our analyses was wind chill temperature, T_{wc} (°C). This was calculated using a combination of air temperature, T (°C) and wind speed, W (m s^{-1}), using the formula (Osczevski and Bluestein 2005),

$$T_{wc} = 13.12 + 0.6215\,T - 13.95\,W^{0.16} + 0.4867\,T\,W^{0.16} \quad (4)$$

The parameters in this equation have been modified from those of Osczevski and Bluestein (2005) to account for the wind speed units used in MicroMet and SnowModel (their units are in km hr^{-1}; these environmental modeling tools use wind speed units of m s^{-1}). The wind chill temperature accounts for the combined effects of cold and wind on a relatively warm body. It describes the temperature a body feels when losing heat due to relatively low air temperatures and wind; it was created for human purposes but has been an effective factor to explain the behavior of other animals (e.g., Courbin et al. 2017). Because wind speed may impact sage-grouse beyond just its contribution to the experienced temperature (e.g., by ruffling feathers and compromising their insulative ability), we considered both wind speed and wind chill temperature in our analyses.

Refugia habitat selection modeling

For our first objective, we modeled sage-grouse winter habitat selection within individual home ranges (third-order scale, Johnson 1980) using paired conditional logistic regression (clogit; Gail et al. 1980; Therneau 2000; Therneau and Grambsch 2015) in the R package "survival." We subset e-obs transmitter locations to 4 per day to match the timing of locations collected by the GeoTrak transmitters. We calculated individual home ranges using 100% minimum convex polygons (MCP) around each bird's winter locations. Then, with each used location, we paired 15 available locations within each bird's winter home range by corresponding date. We reasoned that a 1:15 used: available ratio was a sufficiently large sample size to avoid significant numerical integration error (Northrup et al. 2013). After forming our model, we validated this assumption by comparing coefficients from our model with coefficients from models with used: available ratios of 1:1, 1:4, 1:8, and 1:12 to confirm convergences of estimated parameter coefficients (Northrup et al. 2013).

To identify the operative scales for predictor variables (i.e., the scales at which these conditions were ideally characterized and most likely to influence sage-grouse), we extracted all landscape and weather variables to sampled locations using 8 circular regions of varying radii: 0.1-km (area = 0.03 km^2), 0.2-km (0.13 km^2), 0.4-km (0.50 km^2), 0.8-km (2.01 km^2), 1.6-km (8.04 km^2), 3.2-km (32.17 km^2), 6.4-km (128.68 km^2), and 10.0-km (314.16 km^2). Our aim was to identify the scale at which sage-grouse most likely viewed our landscape predictor variables. Each circular region we considered had relevance to previous research evaluating sage-grouse winter resource selection (Doherty et al. 2008; Carpenter et al. 2010; Smith et al. 2014, 2016, 2019, 2021; Walker et al. 2016). We extracted values of weather variables (Table 2) at sampled locations by corresponding date and across our 8 circular regions. We centered and Z-transformed all variables to ensure model convergence (Becker et al. 1988) and to ease interpretation of main effects and interactions (Schielzeth 2010). As the first step to building our model, we identified the most likely operative scale within each variable category (i.e., topographic, vegetation, or weather; Table 2) by selecting the radius that had the lowest Akaike's Information Criterion (AIC; Akaike 1973) score in single-variable models. We removed unsupported predictor variables when single-variable models had AIC scores greater than random intercept-only models. We further screened variables using Pearson correlation coefficients and did not include variables in the same model if $|r| > 0.6$. We considered several correlated variables that described snow conditions: snow depth (cm), the proportion of the circular area where vegetation protruded above the snow (0–1); and height of vegetation protruding above the snow (cm). To select between these correlated snow variables, we retained the predictor that had the lowest AIC score between single-variable models.

We built our Winter Landscape hypothesis model by considering only landscape variables (topography, vegetation, and snow variables) and used the top model generated with the dredge function from the "MuMIn" R package

(Barton and Barton 2015). Next, we included our predicted snow interactions (Table 1) only if they improved AIC. For our Winter Weather hypothesis model, we considered any weather variables that individually improved AIC over the Winter Landscape model and then used the top model from the dredge function (Barton and Barton 2015). As a final model-building step, we included any predicted weather interactions that further improved AIC (Table 1).

After determining the best model for sage-grouse habitat selection within individual winter home ranges (third-order scale, Johnson 1980), we used the same final predictors to model habitat selection with random "available" points generated at the population scale (second order, Johnson 1980). We defined the population scale using the 100% MCP encompassing winter home ranges for all GPS-fitted grouse. We modeled habitat selection at the second-order scale after first building our model at the third-order scale, because we expected weather to be more influential in affecting grouse behavior within their established winter home ranges than at the larger population scale. Our purpose in comparing second- and third-order models was to assess whether the same variables that influenced sage-grouse behavior within home ranges also played a role in their home range selection within the broader landscape. We allowed operative scales for each parameter in the second-order model to differ from the home range model, and we only removed parameters from the population model if they were correlated (i.e.,$|r|$ > 0.6).

For the purpose of displaying interaction effects in a simple 2-dimensional manner (Figs. 2 and 4), we calculated the predicted selection response on simulated datasets using 20 groups of 1:15 used versus available comparisons for each interaction. In each new dataset, we randomly sampled terrain and vegetation values equally from the first, second, third, and fourth quantiles of observations from the original dataset. We then set weather and snow values in the interaction to minimum, median, and maximum values from the original dataset. All variables not included in each interaction in the simulated dataset were set to their respective mean values from the original dataset.

Activity response modeling

To describe daily sage-grouse behavior, we considered four metrics calculated from the higher-fix-rate, e-obs GPS transmitters from winters 2018/2019 and 2019/2020: (1) average hourly step length (avg.step), (2) daily range area (area.d), (3) distance between night roost locations (dist.), and (4) standard deviation of acceleration (SD.acc). To calculate daily average step length, we subset the daily locations to each hour between civil twilights. We calculated daily range areas using a 100% MCP around each bird's daily locations. Because of the relatively small size of some daily ranges, we found that MCPs did a better job of capturing daily use areas than other home range estimates that require a minimum area covering multiple raster cells (e.g., Brownian bridge or kernel density). In our study, the minimum sage-grouse daily range area was 2 m^2; much smaller than the spatial resolution of most remotely sensed datasets.

We measured roost distance as Euclidean distance between first and last location for each day, representing the distance between each day's roost sites. Lastly, we calculated the daily standard deviation of the magnitude of acceleration, *SD.acc* ($m\ s^{-2}$), (estimated across 5 s during each location fix) using the formula,

$$SD.acc = \sqrt{SDX^2 + SDY^2 + SDZ^2} \quad (5)$$

where SDX^2, SDY^2, and SDZ^2 represent the square of the acceleration standard deviations along the *X*, *Y*, and *Z* planes respectively. We used principal components analysis (PCA; principal function in the R package "psych;" Revelle 2010) to incorporate our multiple movement response variables into a single index representing daily sage-grouse activity. We used the first component of the PCA for our daily sage-grouse activity index (DSA), provided the eigenvalue > 1.0.

Because sage-grouse may respond to environmental changes across multiple days (Pratt et al. 2017), we calculated all weather variables (Table 1) with a "linear predictor" that used α as a weighting factor of the current day's weather value relative to previous days (Gienapp et al. 2005). We considered values for α in increments of 0.1, ranging from 0.1 to 1.0. An α = 1.0 represented the current day's value while α = 0.1 acted as a smoothing parameter representing the trend over the last 30 days (see Fig. 1 in Gienapp et al. 2005). We started calculations from 30 days prior to 1 December, the first day of each winter. For the blizzard variable, we also considered direct blizzard values of one day before and one day after each day, to assess whether sage-grouse changed activity in response to impending precipitation or the previous day's snowfall. For temperature variables, we used the slope between each day's value and the previous 2 days to measure the rate of warming or cooling trends. We also considered day length (hours between civil twilights) as a potential nuance variable of sage-grouse activity. We extracted weather, snow, and landscape variables for each daily range, averaged and weighted by the proportion of cells overlapped by the polygon.

We used information theoretic procedures (Burnham and Anderson 2002) to compare our two predictions to a baseline model of landscape characteristics, and ranked each model using AIC. Because the activity index could not be less than 0 and we predicted variation in activity to be proportional to parameters, as is common with biological data,

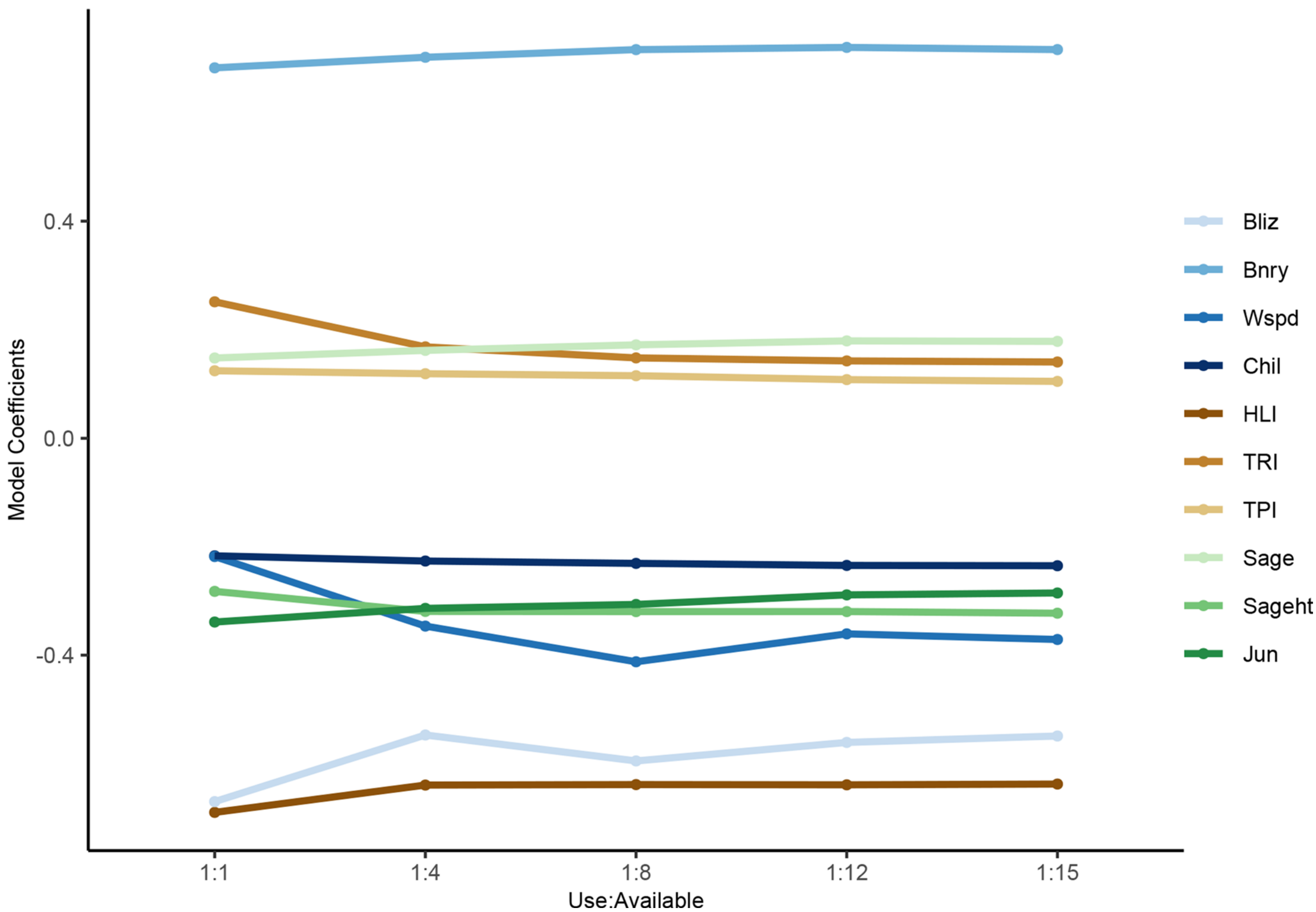

Fig. 1 Comparison of model coefficients from the home range (third order) conditional logistic model to confirm coefficient convergence when using different ratios of used: available locations in greater sage-grouse resource selection modeling, in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA, winters 2018/2019 and 2019/2020

we considered both a generalized mixed-effect model with gamma distribution (link = log) and a linear distribution with the response log-transformed. We compared residual plots to determine the best-fit distribution between these two. Prior to building our three models (i.e., base model and models representing our two predictions), we removed predictor variables if single-variable models had AIC scores that were greater than random, intercept-only models. We then determined the operative α value for each variable by selecting the lowest AIC score in the single-variable models. We used a variable subset approach (Arnold 2010) to determine the most parsimonious behavioral model for each alternative hypothesis, using AIC scores, and we included bird ID as a random mixed effect (interclass correlation coefficient = 0.18). We removed correlated variables ($|r| > 0.6$) by retaining the predictor with the lowest AIC score.

We created our baseline Landscape-only model using topography and vegetation covariates and selected the top model generated using the dredge function (Barton and Barton 2015). Next, we created a Landscape + Snow model (prediction 1 of activity response objective) by adding snow variables (snow depth, binary vegetation protrusion, height of vegetation above the snow, and blizzard conditions with $\alpha < 0.5$) depending on whether each improved AIC over the baseline model. Because there is scant information in the literature regarding sage-grouse winter behavior, for each snow variable, we considered any single interaction with landscape variables that best improved AIC. For our Landscape + Snow + Weather model (prediction 2 of activity response objective) we added weather variables (air temperature, wind chill temperature, wind chill temperature trend, wind speed, and blizzard conditions with $\alpha > 0.5$) representing recent weather trends rather than landscape features. For each weather variable, we considered the one interaction with the landscape variables that most improved AIC. We displayed interactions in figures using the same method of simulated datasets described for the refugia habitat selection model.

Results

Habitat selection model

For the refugia habitat selection objective, we used 16,376 locations from 37 female sage-grouse during winters 2018/2019 and 2019/2020. The Winter Weather model (Table 3) was the top model describing sage-grouse habitat selection within winter home ranges (AIC = 83812.4, Akaike's weight [w_i] = 1.0). The binary variable (proportion of area with vegetation protruding above the snow) was selected to represent vegetation availability in relation to snow depth, using AIC. Of the six interactions considered (Table 1), the only interaction that did not improve model fit was Bnry x Sageht. The Winter Landscape model, which included only topography, vegetation, and snow conditions, had AIC = 84143.5 (ΔAIC = 331.1 w_i = 0.0). Our final habitat selection model had 15 parameters and represented 2.5 individual birds per parameter and 278.2 sampled use locations per parameter. Comparison of model coefficients produced by 1:1, 1:4, 1:8, and 1:12 ratios of use: availability with our top model confirmed that coefficients were stable at the 1:15 ratio (Fig. 1).

The Winter Weather model contained blizzard, wind chill temperature, and wind speed variables (Table 3). Although wind speed is used to calculate wind chill temperature, these two variables were not correlated at the selected operative scales (r = 0.05), and thus, both were included in the model. Within the home-range scale, sage-grouse selected cooler aspects (HLI at grouse use locations ranged from 0.67 to 0.74 within 1.6 km), and selection for cooler aspects was predicted to be greatest during periods of extreme cold (-28 °C; Fig. 2). Sage-grouse also selected flatter topography, and higher terrain positions (50% of use locations occurred between 5.6 and 6.4 TPI within 0.8 km, where TPI > 0 indicates terrain position above mean elevation). Predicted selection for terrain position was greatest during periods when wind speed or available vegetation (Bnry) were higher than their respective medians (4.32 m/s, 0.68, respectively).

Congruent with examples in the literature, sage-grouse selected areas of greater sagebrush height (Dzialak et al. 2013) and canopy cover (Smith et al. 2014), and lower proportions of juniper land cover (Coates et al. 2020). 75% of sage-grouse use locations occurred in areas with < 13.3% sagebrush canopy cover within 0.1 km (Fig. 2),

Table 3 Parameter estimates for predictor variables from conditional logistic regression models that describe daily winter resource selection by greater sage-grouse in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA, winters 2018/2019 and 2019/2020. Values are given from the habitat selection model within home ranges (third-order selection) and within population range (second-order selection) estimates are given in parenthesis wherever values differed from the home range model

Parameter[a]	Operative scale	Estimate	*P*-value
Topography			
HLI	1.6 km	-0.24 (-0.51)	< 0.001
TPI	0.8 km	0.18 (0.26)	< 0.001
TRI	0.1 km	-0.32 (-0.34)	< 0.001
Vegetation			
Jun	0.4 km (0.8 km)	-0.64 (-1.83)	< 0.001
Sage	0.1 km	0.14 (0.27)	< 0.001
Sageht	3.2 km[b]	0.10[b]	< 0.001
Snow			
Bnry	0.1 km (10.0 km)	0.72 (-0.26)	< 0.001
Weather			
Bliz	0.8 km (0.1 km)	-0.55 (0.08)	< 0.001
Chil	0.1 km (10.0 km)	-0.37 (0.21)	0.039 (< 0.001)
Wspd	0.1 km	-0.29 (0.47)	0.002 (< 0.001)
Interactions			
Bnry × TPI		0.09 (0.06)	< 0.001
Chil × HLI		0.05 (0.03)	< 0.001 (0.005)
Chil × Sage		-0.07 (-0.09)	< 0.001
Wspd × TPI		0.08 (0.07)	< 0.001
Wspd × Sage		0.06 (0.22)	< 0.001

[a]Parameter estimates obtained from model with centered and scaled variables. Landscape parameters were measured within operative scales (radii around each location) and included heat load index (HLI), terrain position index (TPI), terrain roughness index (TRI), proportion of juniper land cover class (Juniper), sagebrush (A. tridentata) canopy cover (%; Sage), and height (cm; Sageht). The proportion of area where vegetation protrudes above snow depth (0–1; Bnry) represented the snow parameters. Weather parameters included blizzarding conditions (snow kg/m/s; Bliz), wind chill temperature (°C; Chil), and wind speed (m/s; Wspd)

[b]Variable was not included in population-scale model

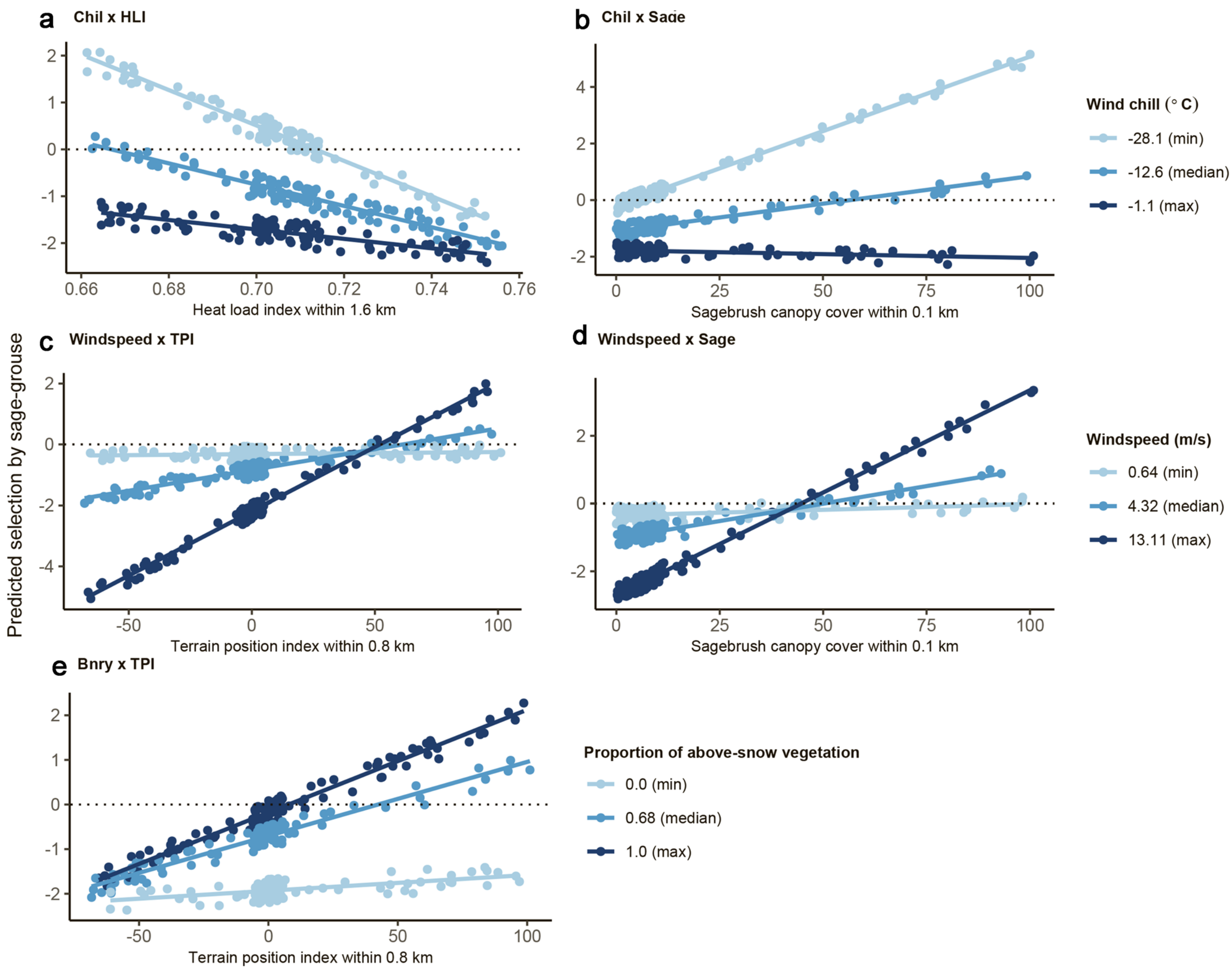

Fig. 2 Predicted sage-grouse winter resource selection response to the interactions between weather or snow conditions and other landscape characteristics using information from the 2018/2019 and 2019/2020 winters in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA. Landscape characteristics included terrain position index (TPI) within 0.8 km, percent sagebrush canopy cover (Sage) within 0.1 km, and heat load index (HLI) within 1.6 km. Weather variables included the proportion of area with vegetation protruding above snow (0/1; Bnry) within 0.1 km, wind speed (m/s; Wspd) within 0.1 km, wind chill temperature (°C; Chil) within 0.1 km. We calculated predicted selection response on simulated datasets using 20 groups of 1:15 used versus available comparisons for each interaction. In each new dataset, we randomly sampled terrain and vegetation values equally from the first, second, third, and fourth quantiles of observations from the original dataset. We then set weather and snow values in the interaction to minimum, median, and max values from the original dataset. All variables not included in each interaction were set to their respective mean values from the original dataset

but sage-grouse showed stronger predicted selection for areas > 50% sagebrush canopy cover when wind speeds were greater than the median of 4.3 m/s or wind chill temperature was below the median of -12.6 °C (Fig. 2). Sage-grouse also selected areas with lower blizzarding, lower wind speeds, and lower wind chill temperatures (Table 3).

When we applied the same parameters to sage-grouse winter habitat selection at the population scale (second order; Johnson 1980), we found similar trends for most parameters, including interactions, and variation in operative scale in only a few variables (Table 3). At the population scale, selection for topography and sagebrush canopy cover were very similar to the home-range scale (Table 3). Avoidance of juniper was much stronger at the population scale (coefficient of -1.83 versus −0.64; Table 3). Sage-grouse selected home ranges with lower proportions of available vegetation (Bnry), higher wind chill temperatures, and greater wind speeds and blizzard conditions, which differed from within home-range selection (Table 3) (Fig. 3).

Behavioral model

We used 27,117 sage-grouse locations from 29 female sage-grouse, subset to an hourly fix rate during daytime hours,

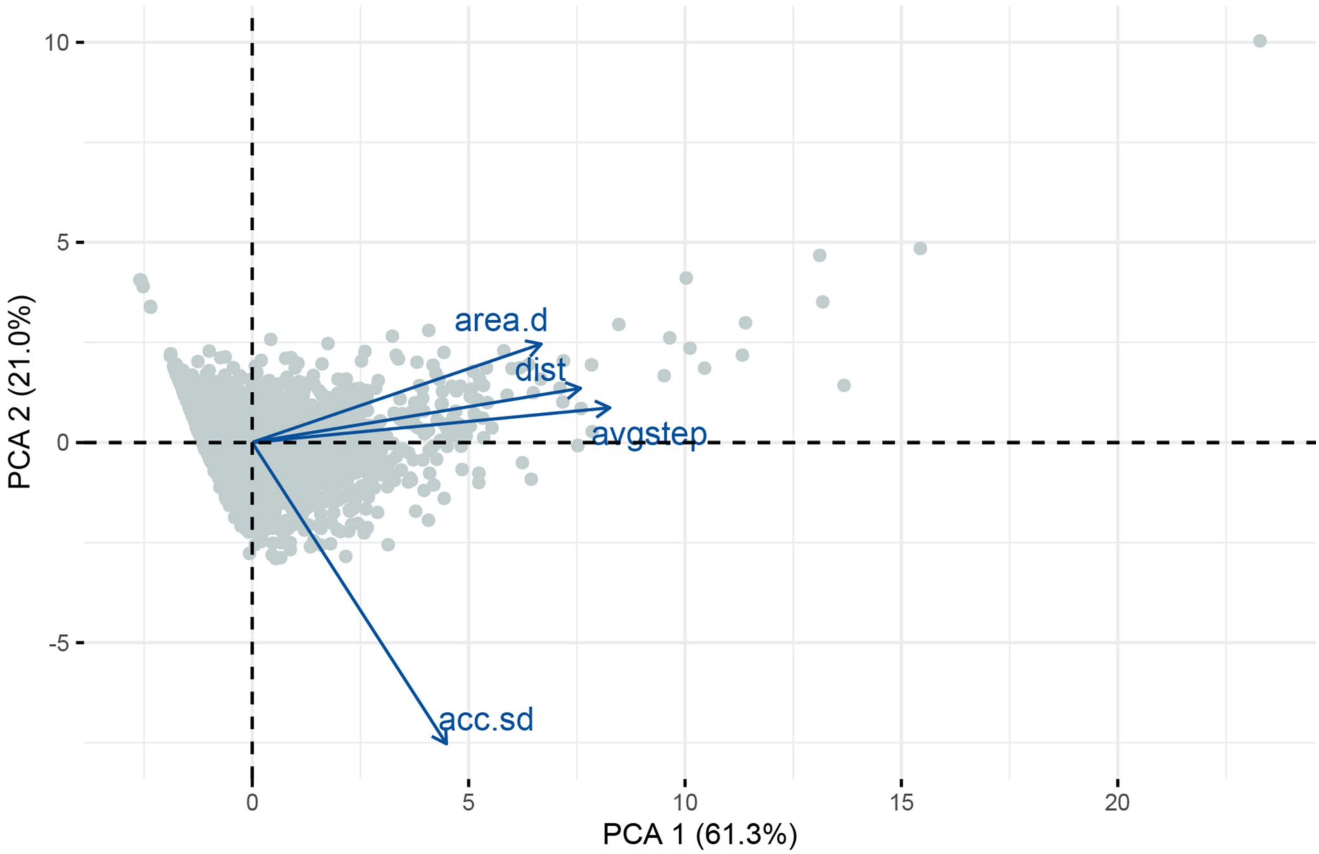

Fig. 3 Biplot of principal components analysis of sage-grouse daily winter movement metrics, including average step length (avg.step), distance between roost sites (dist), daily range size (area.d) and standard deviation of acceleration magnitude (acc.sd), in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA, winters 2018/2019 and 2019/2020

to estimate 3,219 daily ranges from winters 2018/2019 and 2019/2020. The daily average of step-length ranged from 1.6 m to 1,462.2 m with a mean of 130.6 m. Distance between roost sites ranged from 1.1 m to 7,515.8 m with a mean of 716.7 m. Daily range area ranged from 1.0 m^2 to 14.2 km^2, with an average of 0.1 km^2. Daily standard deviation of acceleration ranged from 0.01 m s^{-2} to 0.74 m s^{-2} with a mean of 0.43 m s^{-2}. There was one extreme outlier day removed from the sample after we determined that one female grouse flew to her breeding area mid-winter and then returned within a single day.

In our PCA of sage-grouse activity metrics, principal component 1 (PC1explained 61.3% of the variation. We used PC1 as our daily sage-grouse activity index (DSA), weighted by individual factor loadings in the formula,

$$DSA = 0.904avg.step + 0.855dist + 0.808area.d + 0.148SD.acc \quad (6)$$

After we screened the correlated variables using Pearson correlation coefficients, $Bliz_{\alpha=0.1}$ and $Bnry_{\alpha=1.0}$ were selected to represent the snow variables, and Shrubht was selected to represent shrub vegetation in the models (Table 4). $Bliz_{\alpha=0.1}$ and $Bnry_{\alpha=1.0}$ were moderately correlated (r = -0.52) but removing either one from the model did not largely affect the coefficient estimate of the other, so both were retained. The only weather variable that improved the model over the intercept-only model was the rate of wind chill temperature change over 3-days (Chil.trend3). The Landscape + Snow + Weather model (prediction 2) was the best-fit model for our data (AIC = 8389.5, w_i = 0.972). The second-best model was the Landscape + Snow model (ΔAIC = 7.1, w_i = 0.027), and third was the Landscape-only model (ΔAIC = 234.9, w_i = 0.001). The final model included interactions between $Bliz_{\alpha = 0.1}$ and TPI, $Bnry_{\alpha=0.1}$ and Juniper, and Chil.trend3 and Shrubht. Our final behavioral model had 10 parameters and represented 2.9 individual birds per parameter and 321.9 daily ranges per parameter.

Daily sage-grouse activity levels increased in areas with greater blizzard conditions over the previous month ($Bliz_{\alpha = 0.1}$), greater proportion of juniper land cover (Juniper), more rugged terrain (TRI), and higher terrain positions (TPI; Table 4). Daily activity decreased in areas with greater shrub height (Shrub) and greater proportion of vegetation above snow level ($Bnry_{\alpha=1.0}$). Predicted sage-grouse daily activity increased the most with higher TPI if the month-long

Table 4 Parameter estimates with 95% confidence intervals for predictor variables describing greater sage-grouse daily activity index (ln[DSA]) in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA, winters 2018/2019 and 2019/2020

Parameters[a]	95% CI			
	Estimate	Lower	Upper	*P*-value
Topography				
TRI	0.15	0.11	0.18	< 0.001
TPI	0.20	0.16	0.24	< 0.001
Vegetation				
Shrubht	-0.10	-0.14	-0.07	< 0.001
Juniper	0.06	0.03	0.09	< 0.001
Snow				
$Bnry_{\alpha=1.0}$	-0.20	-0.24	-0.16	< 0.001
$Bliz_{\alpha=0.1}$	0.04	0.001	0.09	< 0.001
Weather				
Chil.trend3	-0.03	-0.06	0.002	0.07
Interactions				
$Bnry_{\alpha=1.0}$ × Shrubht	-0.18	-0.22	-0.15	< 0.001
$Bliz_{\alpha=0.1}$ × TPI	0.04	0.004	0.08	0.029
Chil.trend3 × Shrubht	0.05	0.02	0.08	0.003

[a]Parameter estimates include terrain roughness index (TRI), terrain position index (TPI), shrub height (cm; Shrubht), proportion of juniper land cover (Juniper), and month-long (α = 0.1) blizzarding (snow kg/m/s; Bliz) trends within daily ranges. For each snow and weather variable, we considered the top interaction that improved the AIC score over the non-interaction model

blizzard conditions were also high (Fig. 4 Predicted daily activity decreased in taller shrubs if the proportion of area with above-snow vegetation (Bnry) was high or if the wind chill temperature trend was decreasing (Fig. 4).

Discussion

We employed synthesized daily weather information, vegetation characteristics, and topographic characteristics to evaluate whether greater sage-grouse responded to winter weather by altering habitat selection or adjusting their activity levels. We conducted our study during winters that included above-average snow depths (63rd percentile in 2018/2019 and 91st percentile in 2019/2020 compared to the 30-year average), which provided an opportunity to assess the commonly held assumption that winter weather will not affect sage-grouse habitat selection as long as snow depth does not exceed vegetation height (Call and Maser 1985; Connelly et al. 2000; Crawford et al. 2004). We found that the proportion of vegetation protruding above the snow surface was a significant predictor of winter habitat selection, as previously reported (Call and Maser 1985; Connelly 2000; Crawford 2004). This also agrees with other reports that sage-grouse select taller sagebrush species during winters with greater snow depth (Hanf et al. 1994). We also found strong evidence to support our prediction that sage-grouse would select daily habitat based on both snow and weather conditions. Daily blizzard, proportion of area with vegetation protruding above the snow surface, wind chill temperature, and wind speed affected how sage-grouse selected habitat within home ranges and also home range selection at the population scale (Table 3). Within home ranges, sage-grouse selected areas for lower blizzarding conditions and wind speeds over areas with higher temperatures (Table 3). Wind blew from the south/southeast, during 84% of days during the study period. Seeking shelter from these southernly winds likely explains why sage-grouse selected for cooler, northernly aspects (which might also have taller shrubs for shelter) rather than exposed, south-facing areas (Table 3). At the population scale, sage-grouse selected home ranges with wind-sheltered aspects (lower HLI), flat terrain (lower TRI), near hilltops (greater TPI), and with greater sagebrush canopy cover (Table 3).

Our purpose in modeling daily activity was to provide an alternative method of measuring potential behavioral responses to daily weather conditions. Therefore, we refrained from prescribing activity levels as positive or negative effects of daily weather because we lacked information, such as stress hormone levels or foraging energetics. Higher daily activity levels could be a result of preemptive sage-grouse responses in advance of changing weather conditions, to disturbance from a predator, or in proximity to human activity. Alternatively, low daily activity levels could be the result of a favorable foraging patch, or it could represent a harsh blizzard day when sage-grouse were sheltering in a snow burrow (behavior observed during winter 2019/2020; Back et al. 1987). We found moderate support for our prediction that sage-grouse would have lower daily activity levels as a result of seeking shelter from weather conditions, as evidenced by the lower DSA levels in areas with greater shrub heights during 3-day cooling trends (Fig. 4). However, we found that daily activity levels were more responsive to general snow conditions relative to other landscape features rather than to daily weather. Our results indicate that sage-grouse respond to winter weather conditions primarily by seeking refugia, rather than changing daily activity levels.

Our results validate predictions made in previous literature. The energy requirement of thermoregulation for sage-grouse is lower compared to other gallinaceous birds (Sherfy and Pekins 1994), which may explain the apparent selection for shelter from blizzard conditions and wind direction over greater heat load. In other words, during winter, sage-grouse chose to minimize thermoregulatory costs by avoiding blowing snow and direct winds, rather than by occupying areas with a general potential for higher temperatures through increased solar radiation. At wind chill

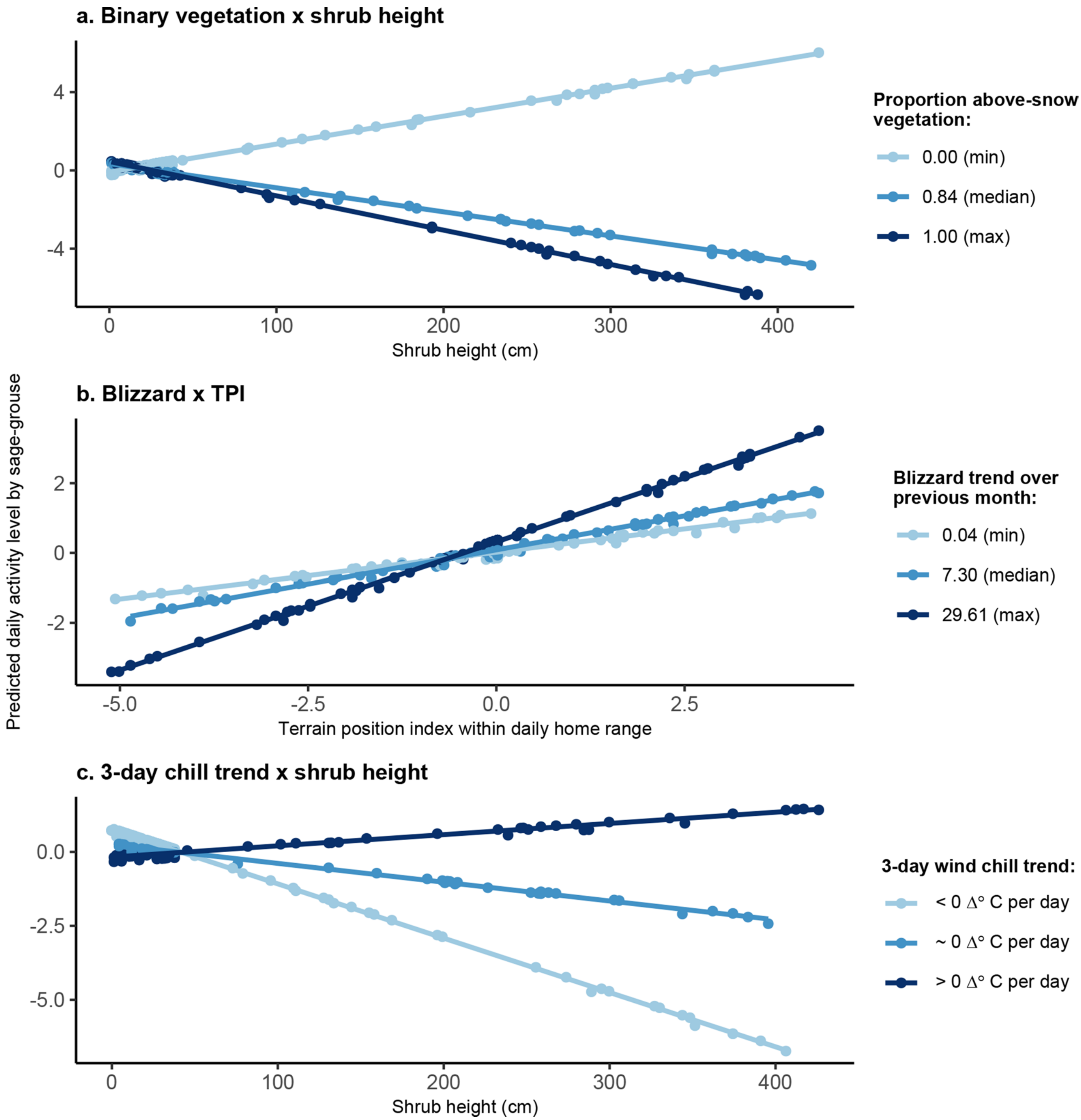

Fig. 4 Interaction trends in predicted daily sage-grouse activity response to snow variables and landscape characteristics in northern Moffat County, Colorado and southern Carbon and Sweetwater counties, Wyoming, USA, winters 2018/2019 and 2019/2020. Snow variables included month-long trends in blizzard conditions (kg/m/s; Bliz) and proportion daily range with vegetation protruding above snow depth (0–1; Binary vegetation). The weather variable was the rate of change in wind chill temperature over 3-day periods (Chil.trend3). Landscape variables included shrub height (cm) and terrain position index (TPI) within each daily range. We calculated predicted selection response on simulated datasets using 20 groups of 1:15 used versus available comparisons for each interaction. In each new dataset, we randomly sampled terrain and vegetation values equally from the first, second, third, and fourth quantiles of observations from the original dataset. We then set weather and snow values in the interaction to minimum, median, and max values from the original dataset. All variables not included in each interaction were set to their respective mean values from the original dataset

temperatures lower than the median (-12.6 °C), we observed increased predicted selection for greater sagebrush canopy cover (Fig. 2). This −12.6 °C wind chill temperature is near the −10 °C air temperature threshold where Sherfy and Pekins (1994) observed increased sage-grouse metabolic rates and where Back et al. (1987) observed sage-grouse more frequently engaged in snow burrowing. While they evaluated air temperature thresholds, Sherfy and Pekins (1995) attributed 50% of metabolic rate increase in adult sage-grouse to wind speeds, with metabolic rates increasing most when air temperatures were also below −10 °C. We observed sage-grouse selection for terrain or vegetation characteristics that minimize wind speed, which would also reduce thermoregulatory costs of sage-grouse. Additionally, we observed predicted selection for higher terrain positions where the proportion of area with above-snow vegetation was higher. This echoes the observation by Hupp and Braun (1989) and others (Remington and Braun 1985) that winters with greater snow depths increase sage-grouse use of high, flat sites and ridges offering greater forage availability.

Our analyses incorporated synthesized weather or environmental variables, a relatively nascent technique in wildlife applications (Glass et al. 2021; Reinking et al. 2022). Synthesized environmental variables combine multiple sources of information to better capture the environmental conditions that wildlife experience. Techniques such as PCA and k-select analysis (Calenge et al. 2005; Franklin et al. 1995) are useful for reducing many intercorrelated variables into fewer uncorrelated variables as long as the resulting metric is biologically interpretable. For environmental variables, models such as MicroMet and SnowModel are preferable to PCA because they can synthesize conditions using realistic physics and meteorological information to predict snow and other environmental conditions at very fine, local scales. The resulting synthesized variables are not just related statistically to individual metrics but represent local conditions more wholistically, thus adding value beyond simple variable reduction.

Synthesized variables can also be considered alongside individual components that may affect animals in different ways. Our results suggest that sage-grouse respond to wind speed differently than they do to wind chill temperature, even though wind speed was a component of wind chill temperature. Wildlife researchers can take advantage of this new technology by considering weather and other environmental variables beyond simple meteorological metrics (e.g., wind chill or heat index temperatures instead of air temperature, or blizzarding instead of general precipitation).

Our results underscore the importance of examining winter habitat at narrower temporal scales than the entire winter season. In our study, 75% of used locations within sage-grouse winter home ranges had < 15% sagebrush canopy cover. If we had only considered selection for sagebrush cover at a season-long scale, we most likely would have overlooked the periods of extreme cold and deep snow when sage-grouse selected greater sagebrush canopy approaching 100% within 0.1 km (Fig. 2). Smaller temporal scales are necessary for identifying refugia habitat that may be expected to confer greater winter survival, even if these habitats have a small spatial extent or are infrequently used (Dzialak et al. 2013; Adam et al. 2015).

The ability of sage-grouse populations to withstand severe weather may vary regionally depending on the proportion of available refugia habitat. If sage-grouse are unable to select refugia from severe weather, it may explain the high mortality reported in some winters (Moynahan et al. 2006; Anthony and Willis 2010). Alternatively, the presence of adequate refugia may explain why weather was not found to have a significant impact on winter survival in other regions (Zablan et al. 2003; Dinkins et al. 2017). Other sage-grouse populations may respond to weather differently based on available landscape characteristics, or their populations may be more limited by summer refugia habitat when dry conditions reduce available forage (Donnelly et al. 2018). However, our results lend support to the idea that landscape sustainability for species that rely on high annual survival may depend on habitats that populations select when weather conditions are most limiting (Maron et al. 2015).

Climate change is predicted to reduce the range of sagebrush in the West through a combination of reduced snow melt and shifting precipitation patterns leading to drier, hotter summers and increased fire frequency (Ziska et al. 2005; Homer et al. 2015; Palmquist et al. 2016). If sagebrush cover is, indeed, reduced, sage-grouse could lose important habitat during winter as well as breeding seasons (Wolf and Broughton 2016). As sage-grouse habitat becomes increasingly fragmented and lost to climate change and human development (Walker et al. 2020), additional research into quantifying weather refugia for wintering sage-grouse populations may provide important information and more support for the conservation of sagebrush for sage-grouse winter habitat (Beck et al. 2009; Poessel et al. 2022).

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Data availability Final datasets used in model creation are provided as electronic supplementary material. Weather datasets were generated from SnowModel and are not publicly available because they were privately purchased from Colorado State University. Animal coordinate datasets belong to University of Wyoming and are shared with Wyoming Game and Fish Department; they are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no conflict of interest.

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