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Received: 16 February 2022 | Accepted: 23 February 2022

DOI: 10.1002/ecs2.4146

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Greater sage-grouse habitat selection varies across the marginal habitat of its lagging range margin

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Funding information
Nevada Department of Wildlife; U.S. Bureau of Land Management; Alton Coal, LLC

Handling Editor: Debra P. C. Peters

Abstract

Studying wildlife–habitat relationships at the edges of their range can provide valuable insights into the environmental factors limiting wildlife distributions and most likely to drive extirpations and range shifts in response to landscape change. Yet the relative impact of those factors is likely different along the range margin, so it is important to identify the limitations to suitable habitat at both regional and local scales. Some of the most drastic impacts of large-scale landscape changes in North America have occurred and are forecasted in the sagebrush steppe ecosystems, where species unable to seek new habitat in the fragmented landscape will be vulnerable to climatic extremes, vegetation community shifts, and anthropogenic land use change. One of the species likely under major threat from landscape changes is the greater sage-grouse (*Centrocercus urophasianus*), a sagebrush obligate with habitat constraints that make it susceptible to habitat loss impacts as sagebrush systems contract and fragment at their southern range margin, already naturally fragmented. In this study, we evaluated factors of topography and land cover directly impacting habitat selection by sage-grouse in four study areas along their lagging range edge. We used >116,000 GPS locations from >90 grouse across four study areas in southern Utah and Nevada from 2014 to 2020 in habitat selection analyses using random forest models. Our results showed that sage-grouse exploit topography and sagebrush cover, possibly to break predator sight lines and moderate the risk posed by avian predators using tree perches, complicating the effects of tree cover and conifer encroachment into sagebrush habitat. We found similar trends across all four study areas, suggesting sage-grouse along the southern range margin face similar limitations. However, the effects were nonlinear and varied—models trained in one study area were only moderately successful at predicting selection in others. The local idiosyncrasies along this southern range margin indicate a need for place-based conservation for sage-grouse and other potentially imperiled species. Incorporating new understandings of local impacts will refine regional and range-wide models and support efforts to effectively create habitat and plan for range shifts by vulnerable species in response to environmental change.

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KEYWORDS
Centrocercus urophasianus, Great Basin, habitat selection, random forest, range margins, sagebrush steppe, sage-grouse, used-available

INTRODUCTION

Range margins are critical environments to study in order to understand the factors limiting wildlife habitat and distribution and to predict how landscape changes are likely to drive species redistributions (Oldfather et al., 2020; Seabrook et al., 2014; Travis & Dytham, 2004). Range margins tend to have lower habitat quality and populations there are more at risk of extirpation (Aldridge et al., 2008). The risk to range edge populations is even greater when compounded by fragmented habitat, which is common to range margins and increases population isolation and extinction probability and reduces the capacity to move or adapt to new environments (Bush et al., 2011; Pearson et al., 2009). Range margins can therefore act as natural laboratories, as conditions there may portend the effects of future changes elsewhere and their isolated, tenuous nature can help identify some of the most important factors limiting wildlife habitat.

The sagebrush steppe ecosystem is among the most threatened in North America; wildlife that reside there are threatened by increasing habitat fragmentation and decreasing habitat quality. Invasive species altered fire regimes, climate change, ongoing drought, and land conversion for an increasing human footprint all contribute to diminishing wildlife habitat. By some estimates, the range of the sagebrush steppe ecosystem has been reduced by more than 50%, and wildlife species that depend on it are imperiled by its loss (Connelly et al., 2004; West, 1983b). Those that occupy its edges are likely especially at risk, as they will face continuing habitat degradation. Yet even along that range margin, there is likely variation in habitat suitability and in the degree to which populations are threatened by fragmentation impacts and future ecosystem threats.

One of the species likely under greatest pressure from climate and habitat changes is the greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse"), a native grouse and sagebrush specialist that has become emblematic of threats to wildlife across the semiarid West. Though its distribution covers large areas of North America, its relatively narrow habitat constraints as a sagebrush obligate make it susceptible to habitat loss due to land cover change (Coates et al., 2018; Knick et al., 2013). Sagebrush range extent has collapsed considerably since European expansion into western North America due to changing fire regimes, livestock grazing, agricultural development, and pinyon–juniper forest encroachment (Aldridge et al., 2008; Braun, 1998; Juliusson & Doherty, 2017; Knick et al., 2003; M. A. Schroeder et al., 2004; Wisdom et al., 2011) and is likely to contract at its southern range margin in response to climate change (Kleinhesselink & Adler, 2018). Climate change impacts may be especially notable along the sage-grouse southern range margin in the basin and range province of southern Utah and Nevada, where sage-grouse habitat is naturally fragmented by north–south trending mountain ranges into discontinuous sagebrush-dominated valleys. Along this range margin, an increasingly hot and arid climate may decrease the availability of preferred forage and shelter from extreme temperatures while also increasing sage-grouse vulnerability to predation due to pinyon–juniper (*Pinus edulis*, *P. monophyla*, and *Juniperus* sp.) forest encroachment (Baruch-Mordo et al., 2013; Coates et al., 2017; Severson et al., 2017). In order to understand sage-grouse responses to climate, predict future range shifts, and aid conservation of sage-grouse, it is essential to focus more research on the southern, lagging range edge and the factors impacting habitat selection there (Hampe & Petit, 2005; Oldfather et al., 2020; Travis & Dytham, 2004; Walther et al., 2002).

Considerable past research has identified abiotic and biotic requirements for sage-grouse habitat (e.g., Knick et al., 2013; Wisdom et al., 2011; Yost et al., 2008). Yet much of that work has focused at range-wide scales to gain valuable knowledge about general trends and habitat needs (Aldridge et al., 2008). Some research has addressed sage-grouse habitat at range margins, though little research has examined their southern range margin. While sage-grouse generally live in semiarid, sagebrush-dominated landscapes, yet there is regional variation in macroecological variables within those constraints across their range and they likely experience different bioclimatic limitations at range margins than in the range core (Aldridge et al., 2008; Doherty et al., 2016). There is likely similar variation in small-scale drivers of selection even within regions of sage-grouse range, where the most important regional-scale factors are not the same as those affecting individual populations or discrete habitats (Dahlgren et al., 2019; Picardi et al., 2020).

Recently, efforts to improve sage-grouse habitat in the southern end of their range have focused on removing pinyon and juniper woodlands that have expanded into areas previously dominated by sagebrush (Frey

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et al., 2013). We examined how sage-grouse are likely to respond to these efforts to increase sagebrush habitat. While the negative impacts of pinyon–juniper forest encroachment on sage-grouse are well documented, we hypothesized that there are features of topography and other land cover types that complicate that effect. In particular, we hypothesized that sagebrush cover and rugged terrain may mitigate the threat of predation due to tree cover. Range edges in heterogeneous landscapes are constrained by complex interactions of environmental factors that are not uniform along that range edge (Boakes et al., 2018; Oldfather et al., 2020). For that reason, we also hypothesized that sage-grouse habitat selection is driven by similar factors across our study region, but with variation between study areas in the most impactful variables and in specific thresholds.

METHODS

Overview

We used a multistep process using random forests (RFs), a simple machine learning algorithm (Breiman, 2001), to test the topographic and land cover characteristics driving sage-grouse habitat selection in four study areas across the southern Great Basin of Utah and Nevada. We performed model validation on withheld data within each study area. We then tested the ability of models from each study area to predict the data from every other study area for out-of-sample validation. We performed all analyses using the program R (R Core Team, 2020) and associated packages.

Study region

Our study region included several discrete areas of sage-grouse habitat along or near their southern range margin in southern Utah and Nevada. In Utah, that included the Panguitch, Bald Hills, and Hamlin Valley Sage-Grouse Management Areas (SGMAs; Utah Public Lands Policy Coordination Office, 2019). Sage-grouse habitat in this region tends to be fragmented at large scales by Basin and Range province mountains. In Nevada, we worked in the northern end of Hamlin Valley within the Lincoln population management unit (PMU) and the Steptoe/Cave PMU (Emm et al., 2019) (Figure 1). The total study region spanned 37.2–39.1°N latitude and 112.4–114.9°W longitude. Elevation across the entire area ranged from 1600 to 2800 m. During the study period, our study areas had an average temperature of 8.0°C in Panguitch, 8.1°C in the Bald Hills, 10.3°C in Hamlin, and 7.4°C in Steptoe/Cave. The study areas received an average of 378 mm of precipitation in Panguitch, 350 mm in Bald Hills, 302 mm in Hamlin, and 277 mm in Steptoe/Cave (PRISM, 2020).

Each of the valleys in our study area was dominated to varying degrees by species of sagebrush (*Artemesia* sp.). In the most xeric valleys, sagebrush species accounted for more than 90% of vegetation interspersed with bare ground and sparse grasses and forbs. In more mesic areas, native bunchgrasses, rabbitbrush (*Ericameria* sp.), and a variety of forbs were present, though sagebrush was still the dominant shrub species. The sagebrush was mostly *A. tridentata wyomingensis* and other *A. tridentata* subspecies, with *A. nova* common in the more xeric habitats. Our study region represented much of the range of conditions prevalent in the Great Basin–Colorado Plateau sagebrush semidesert, a subset of the Intermountain West region, but generally more xeric than much of sage-grouse range in the sagebrush steppe (West, 1983a). Across the study region, the valleys were fringed with mixed woodlands of pinyon pine and juniper, while higher elevation areas included quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus* sp.), juniper, spruce (*Picea* sp.), and fir (*Abies* sp.). There were also some high-elevation sagebrush patches used by sage-grouse that migrate upward during the summer. In each study area, some sage-grouse relocate seasonally, while others do not apparently dramatically change their home range.

Data collection

From 2014 to 2020, we captured sage-grouse at night during minimal moon illumination using spotlights and dip nets in October–December and late February–mid-April. We searched both in small groups on foot and on all-terrain vehicles, depending on accessibility and acceptable landscape use in that area, similar to Giesen et al. (1982). When handling, birds were aged, sexed, and examined for injury. Any bird with injury or showing distress was released. We fitted birds with a rump-mounted, solar-powered GPS transmitter (22 g; GeoTrak, Apex, NC; Microwave Telemetry, Columbia, MD) with adjustable Teflon straps that included a section of elastic stitched in to stretch with the bird's movements (not to accommodate the size of the bird). Once fitted, we released the bird and waited for it to fly away without impairment. On the rare occasion that a bird showed an inability to adjust to the transmitter, such as exhibiting short uneven bursts of flight followed by a hard landing, we recaptured it, cut off the transmitter, and released the bird.

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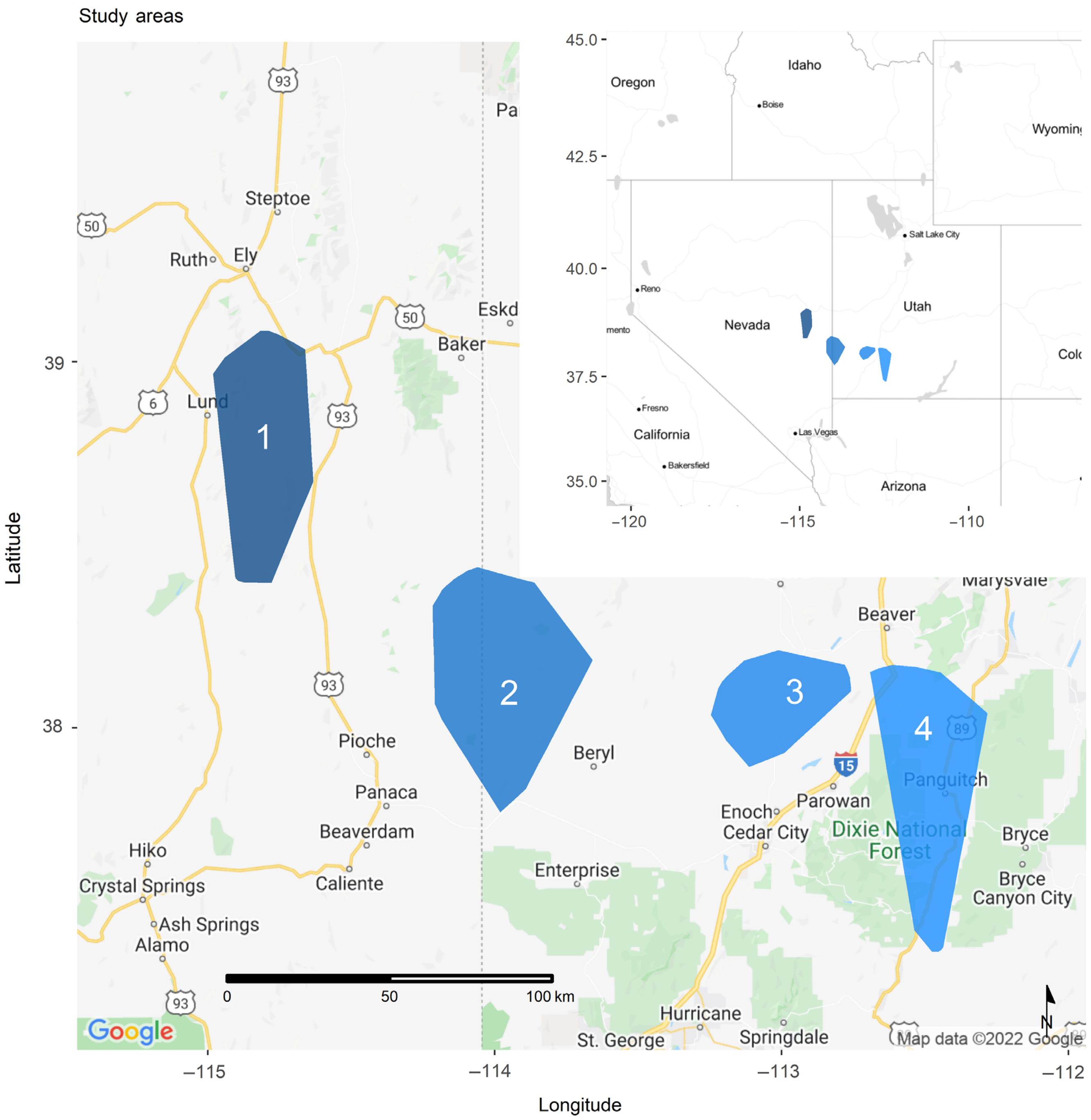

FIGURE 1 Four study areas and their context in Utah and Nevada, drawn here by a minimum convex polygon around the data points used in our analyses. Study areas are (1) Cave/Steptoe Valleys, (2) Hamlin Valley, (3) Bald Hills, and (4) Panguitch.

Transmitters were programmed to collect four GPS locations per day: dawn, mid-day, dusk, and night. During data processing, we removed points from the dataset that were acquired from any individual with fewer than 100 successful fixes or collected within 48 h postrelease. After also removing erroneous points that were clear outliers, our dataset included 116,310 points from 96 individuals (median $n = 1398$/individual) during the period of 2014–2020. Of those 96 sage-grouse, 31 were in Bald Hills (43,449 locations), 12 were in Cave (10,375 locations), 29 were in Hamlin (44,950 locations), and 24 were in Panguitch (17,536 locations). We estimated individual 90% home ranges using a kernel density estimator with the default settings from the R package *adehabitatHR* (Calenge, 2017) and examined the habitat within those estimated home ranges to evaluate third-order selection (D. H. Johnson, 1980).

Our used-available model design required random "availability" points to compare with the available

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environment (McDonald et al., 2013). To create these points, we generated randomly sampled points from within each individual sage-grouse's home range at a 1:10 used-available points ratio. Across all study areas and individuals, this resulted in more than 1,339,000 availability points.

Environmental covariate data

For all four study areas, we used land cover data from the most recent land cover type models from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE; Rollins, 2009), downloaded over the extent of our study region (Table 1). To measure the impact of trees, we calculated distance to any pixels classified as some type of trees or woodland and the density of those pixels within 400- and 800-m moving windows. Past research has shown that sagebrush patch size can be important (Wisdom et al., 2011), so we calculated sagebrush patch contiguity (CONTIG) and core area index (CAI) using the R package *landscapemetrics* (Hesselbarth et al., 2019) with all sagebrush cover types in a binary raster. The CONTIG measures the spatial connectedness of pixels comprising a land cover patch. The CAI measures the percent area of a patch (here, of sagebrush) that is not adjacent to a nonmember land cover type. Its values can be as low as 0 (when there is no core area) and approach 100 with increasing patch interior. We used CONTIG and CAI rather than sagebrush cover density (as we did for tree cover) because a pixel could have a very high sagebrush cover density value whether it is within a sagebrush patch, which is less ecologically meaningful than the nature of sagebrush patches. On the other hand, distance to trees and neighborhood tree cover density impact selection whether or not a sage-grouse is in a treed pixel.

We downloaded elevation data for the extent of our study region at 10-m resolution using the R package *elevatr*, which accesses Amazon Web Services (Hollister et al., 2017). From that digital elevation model (DEM), we calculated metrics of topographic position, heterogeneity, and slope. Topographic position index (TPI) is calculated as the relative elevation of any one cell compared with the cells around it within a user-specified window size, showing whether a DEM cell is part of a hill, valley, or flat ground (Jenness et al., 2013). We also calculated a topographic heterogeneity index (THI) by summing the absolute value of TPI within that same window size for a measure of overall ruggedness. We calculated TPI and THI, each at window radii of 50, 200, and 400 m. More information about the values of environmental covariates for each study area is available in Appendix S1: Table S1.

Model development

We built models within each of the four study areas to evaluate regional variation. We also split the data into three seasons: breeding (March–May), summer (June–September), and fall/winter (October–February), resulting in models for each season and models across all seasons. Though seasonality was not our primary focus, it is well established that sage-grouse require different seasonal habitats (Connelly et al., 2000; Dahlgren et al., 2016). Including season as part of the analysis allowed us to detect possible effects of seasonality on our other findings and make more

TABLE 1 All predictor variables used in data analysis.

Variable	Name	Category	Theoretical range	Units
Sagebrush patch core area index	CAI	Land cover	0–100	Percent
Sagebrush patch contiguity	CONTIG	Land cover	0–1	None
Distance to woodland/forest	TREEDIST	Land cover	0–∞	Meters
Tree density, 400-m radius	TREEDEN400	Land cover	0–1	Proportion
Tree density, 800-m radius	TREEDEN800	Land cover	0–1	Proportion
Topographic position index, 50-m radius	TPI50	Terrain	−∞ to ∞	Meters
Topographic position index, 200-m radius	TPI200	Terrain	−∞ to ∞	Meters
Topographic position index, 400-m radius	TPI400	Terrain	−∞ to ∞	Meters
Topographic heterogeneity index, 50-m radius	THI50	Terrain	0–∞	Meters
Topographic heterogeneity index, 200-m radius	THI200	Terrain	0–∞	Meters
Topographic heterogeneity index, 400-m radius	THI400	Terrain	0–∞	Meters
Slope	Slope	Terrain	0–90	Degrees

Note: Land cover variables are at 30-m horizontal resolution and terrain variables are at 10-m horizontal resolution.

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precise evaluations. We analyzed the sage-grouse habitat selection using RF models, a tree-based ensemble machine learning classifier (Breiman, 2001). Random forest is a nonparametric method that builds hundreds or thousands of classification trees, each using a bootstrap sample to train the model, while a subset is withheld as an out-of-bag testing dataset for each finished tree in the forest. Compared with the more commonly used resource selection function (RSF), RF is better able to detect nonlinear effects, is less prone to problems of autocorrelation because it does not assume independence of samples, and by default considers interactions among variables (Biau, 2012; Breiman, 2001; Cutler et al., 2007; Farrell et al., 2019). It has been successfully used to model species distributions and animal habitat selection (Carrasco et al., 2014; Doherty et al., 2016; Evans & Cushman, 2009; Schwalm et al., 2016; Shoemaker et al., 2018; Zhang et al., 2019). Random forest includes in its process withholding a subset of data to test the trained classification trees, but we took additional steps to ensure thorough model training and validation. First, we created a randomly assigned training dataset with which to develop models using 70% of the data within each season and study area. We used the R package *ranger* (Wright & Ziegler, 2017) to build RF models using leave-group-out k-fold cross-validation (LGOCV) with the data grouped by individual sage-grouse ID to strengthen the model's internal evaluation process and avoid overfitting. In each of the folds, the data were divided by using three quarters of the individuals' data for model training and the remaining for the cross-validation. To further avoid overfitting, we increased the minimum node size in each tree of the RF from the default of 1 for RF classification to either 20 or 50 points in model tuning. We also tuned the models by allowing the number of variables randomly selected for evaluation at each node (*mtry*) to vary between 3, 4, 5, and 8, whereas the default is the square root of the total number of covariates. We selected the best overall model by model accuracy. In both classification analyses such as RF and in presence-only models like RSF, it can be problematic to oversample from one class of the response variable (Boyce, 2006; C. Chen et al., 2004; MacKenzie, 2005). Therefore, for each study area–season combination, we randomly sampled from the available points for each individual for comparison with GPS point detections for that individual, so that each model had a 1:1 used-available ratio and avoided the problems of an imbalanced design (Cushman et al., 2010; Evans & Cushman, 2009; Valdes-Donoso et al., 2017). We repeated that sampling process without replacement until all "available" points were included in models and averaged the models' predictions during model evaluation (similar to Khalilia et al., 2011).

To examine the nature of the variables' impact, we visualized some of the most ecologically relevant relationships with partial dependence plots using the R package *pdp* (Greenwell, 2017) and plots of feature contribution (Kuz'min et al., 2011; Palczewska et al., 2014; Robinson et al., 2017) using the R package *rfFC* (Palczewska & Robinson, 2015). Both methods are useful for interpreting RF models. Partial dependence plots show the impact of one or two variables when the impact of all other variables is held at their mean effect. This is useful for visualizing the basic structure of relationships and of targeted two-way interactions. Feature contribution plots compute separately each point's relationship to other variables, accounting for variable interaction rather than averaging its effects (Palczewska et al., 2014; J. W. Schroeder et al., 2020). The response in feature contribution plots for a classification model shows the increase or decrease in probability for each value of the predictor variable (here, of sage-grouse habitat selection) compared with the predictions for the rest of the dataset.

Comparison with RSF

In addition to the RF models, we modeled sage-grouse habitat selection using RSF models. Resource selection functions are more commonly used for habitat selection analyses, so we included them for comparison with the RF models' ecological findings and predictive performance. We used individual sage-grouse ID as a random effect with a random intercept, fitted using the R package *lme4* (Bates et al., 2012). We selected the best fit models in an information theoretic framework using Akaike information criterion corrected for small sample size (Burnham et al., 2011). We found the best-fit model for both the entire study region and within each study area to examine place-based drivers. We excluded from consideration any models with excessive correlation between predictor variables ($r > 0.5$) and dropped variables with a variance inflation factor greater than 10 (Naimi et al., 2014).

Model validation

After training and selecting the best-fitting models using RF, we evaluated model performance in predicting the withheld 30% of the dataset true skill statistic (TSS). True skill statistic can theoretically range from −1 to 1, with 0 being a totally uninformative model. Because there is argument that metrics like TSS may be inappropriate for a habitat selection study (Fieberg et al., 2018; C. J. Johnson et al., 2006), we also included the model's sensitivity. In addition to those evaluation metrics, we also built calibration plots for each of the models, calculating the correlation between expected and observed probability of selection, where a higher

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correlation indicates better model performance (Fieberg et al., 2018). We repeated the model validation process for each iteration of every study area–season model combination and recorded the average by each metric.

Study area comparison

To compare across study areas and determine variation in habitat selection across the region, we first simply qualitatively compared the most important variables and their general effects among the resulting models. Further, we tested model predictive performance from one study area to another with the RF models. We used the model for each study area to predict the datasets for each of the other study areas, evaluating their predictive performance by TSS, sensitivity, and calibration correlation. A poor fit across study areas would indicate unique selection criteria for that study area and demonstrate differences in sage-grouse habitat selection across their southern range margin.

RESULTS

The presence of trees influenced sage-grouse selection among the study areas, but differently for each area. In all four study areas, linear distance to trees (TREEDIST), the density of trees at 800 m (TREEDEN800), or the density of trees at 400 m (TREEDEN400) were among the most important variables influencing sage-grouse selection, as measured by mean decrease in Gini score (Table 2). In each study area, there was a clear negative effect of TREEDEN800 (Figure 2a) and TREEDEN400 (Figure 2b), as sage-grouse selected for low tree density. This effect was nonlinear, and for each study area, there were different rates of change in selection across tree density. For example, in the Bald Hills area, sage-grouse selection was about <1% more likely at 15% tree cover (TREEDEN800) than predicted by the rest of the Bald Hills dataset, while in Panguitch at the same level of tree cover, sage-grouse selection was 8% *less* likely. However, in all study areas there was selection for landscape with <4% tree cover, an overall trend of decreasing selection with increased tree cover, and a negative association with proximity to trees in all study areas but Panguitch (Figure 2c). In each study area, tree cover between 30% and 40% was associated with less pronounced avoidance (though still not selection) compared with higher or somewhat lower cover.

Our results demonstrate important roles of topography and sagebrush cover, including in changing or moderating the negative impact of trees. Topographic heterogeneity index at 400 m (THI400) was consistently one of the most important variables in the models. Most importantly, sage-grouse selected slightly heterogeneous terrain over flat or more rugged terrain in the Bald Hills, Cave, and Panguitch study areas as measured by THI400 (Figure 3a). Similarly, sage-grouse selected terrain that is slightly lower in elevation than the surrounding area within a 200-m window and tended to avoid high points or very low points in the Cave, Hamlin, and Panguitch study areas (Figure 3b). We found that slope was often important (among the top six variables in 10 of 12 study area–season model combinations), but it was always less influential than at least one other topographic variable (e.g., TPI and THI) based on mean decrease in Gini score (Table 2). Slope had a generally negative relationship with sage-grouse

TABLE 2 Top six most important environmental variables in each study area–season model combination, measured by mean decrease in Gini impurity index.

Study area	Season	Important variables
Bald Hills	Breeding	TREEDIST, TREEDEN800, TREEDEN400, THI400, THI200, Slope
Bald Hills	Summer	TREEDEN800, THI400, TREEDIST, TREEDEN400, THI50, THI200
Bald Hills	Fall/winter	TREEDIST, TREEDEN800, THI400, TREEDEN400, THI200, THI50
Cave	Breeding	TREEDEN800, THI400, TREEDIST, THI200, Slope, TREEDEN400
Cave	Summer	TREEDIST, THI400, TREEDEN800, Slope, TREEDEN400, THI200
Cave	Fall/winter	TREEDIST, THI400, TREEDEN800, Slope, THI200, THI50
Hamlin	Breeding	THI400, TREEDIST, TPI400, THI200, Slope, TPI200
Hamlin	Summer	THI400, TREEDIST, THI200, Slope, TPI400, TREEDEN800
Hamlin	Fall/winter	TREEDIST, THI400, THI200, TREEDEN800, TPI400, Slope
Panguitch	Breeding	TREEDEN800, TREEDIST, THI400, TREEDEN400, Slope, THI200
Panguitch	Summer	TREEDEN800, THI400, TREEDEN400, THI200, Slope, TPI400
Panguitch	Fall/winter	THI400, TREEDEN800, Slope, TREEDEN400, THI200, TPI400

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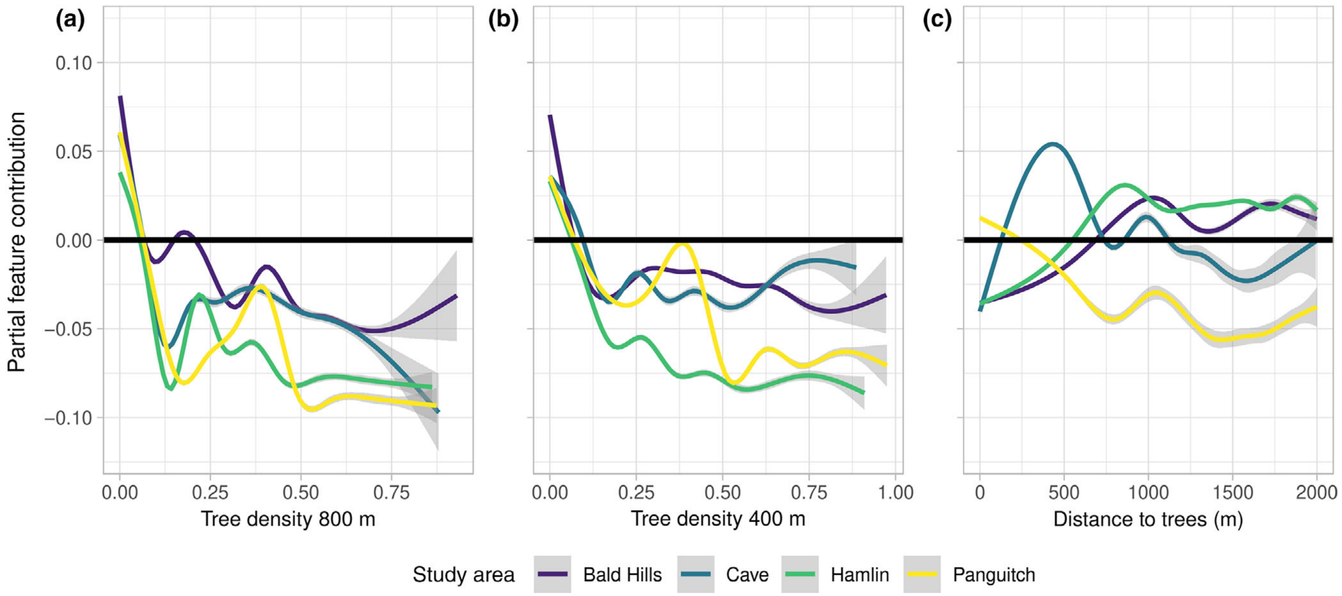

FIGURE 2 Feature contribution of three variables of tree cover in models across four study areas. (a) The contribution of density of treed pixels in an 800-m radius (TREEDEN800); (b) the contribution of density of treed pixels in a 400-m radius (TREEDEN400); (c) the contribution of the distance to trees (TREEDIST). Feature contribution measures how a variable impacts the random forest model's prediction of a point used versus available status at each value of that variable. A positive value indicates a greater probability of the point being "used" compared with the prediction made by the rest of the model. The solid black line at feature contribution = 0 indicates the point at which selection and avoidance are equally likely.

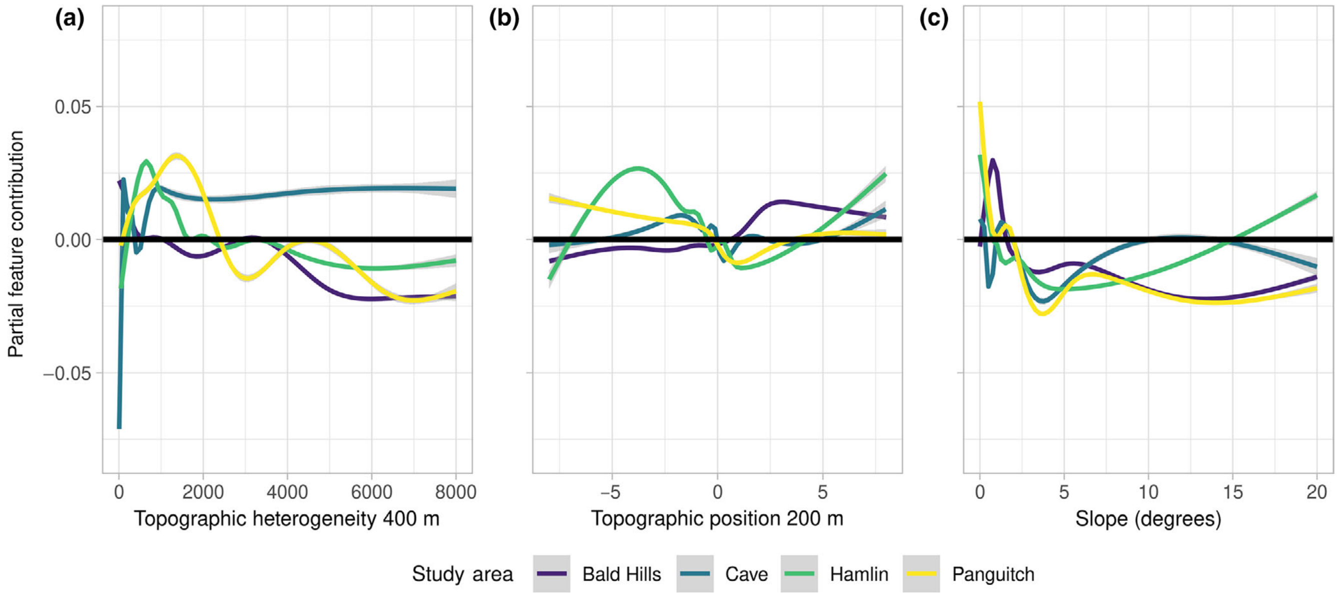

FIGURE 3 Feature contribution of three topographic variables in the models across four study areas. (a) The impact of topographic heterogeneity within a 400-m radius (THI400); (b) topographic position compared with a 200-m radius (TPI200); and (c) topographic slope.

habitat selection, though its effect was uneven (Figure 3c). Two-way partial dependence plots further demonstrated the influence of topography on selection. For any given distance to trees, sage-grouse habitat selection was most likely in moderately heterogeneous terrain and in slightly low-lying, protected areas (Figure 4a).

Further, the RF models suggest that sagebrush cover plays a role in moderating the impact of TREEDIST. Sagebrush patch CAI and patch CONTIG were among the least important variables in the RF models, but two-way partial dependence plots illustrated their impact; for any given distance to trees, sage-grouse selection was

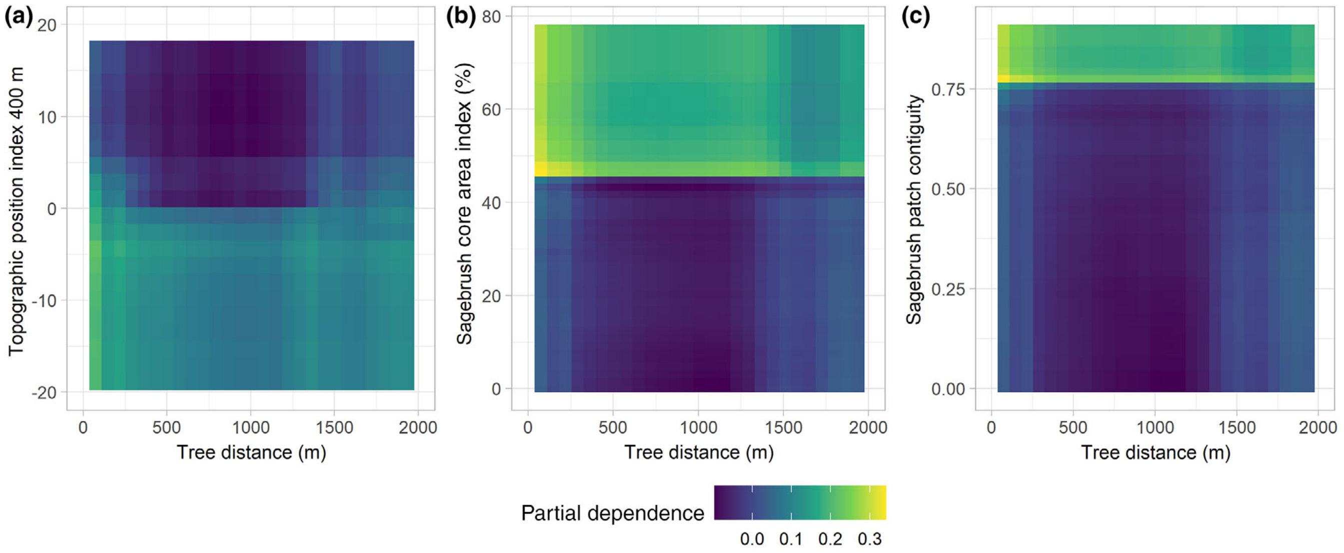

FIGURE 4 Partial dependence of (a) topographic position index within a 400-m radius (TPI400), (b) sagebrush core area index (CAI), and (c) sagebrush patch contiguity (CONTIG) with data from all four study areas. Partial dependence (measured by yhat or ŷ) measures the impact of one variable on the predicted outcome (here, probability of selection) of the response. A higher value corresponds to a higher probability of selection.

more likely in areas of higher CAI (Figure 4b) and CONTIG (Figure 4c).

Seasonality

Predictive power was greater when the models were built with data from only one season (Table 3), suggesting that within each season, sage-grouse have differing habitat selection criteria. In each season, sage-grouse selection decreased as tree density within 400 m increased (TREEDEN400; Figure 5b). This effect was strongest in the fall/winter season and weakest in the breeding season. In each season, there was a positive influence on selection at low tree cover; birds selected areas with <2% cover in summer and breeding seasons and <11% in fall/winter, in which we found by calculating local minima in feature contribution. Selection for distance to trees in each season had a nonlinear effect. In breeding and fall/winter seasons, sage-grouse avoided areas close to trees, but in summer, they selected areas close to trees and avoid areas very far from trees (Figure 5c).

There was a mixed effect of sagebrush core area among the seasons; with increasing CAI, this factor's contribution to modeling habitat selection increased for the breeding and fall/winter seasons, with positive effects above moderately high CAI values; this effect was not present for the summer season (Figure 6a). Sagebrush CONTIG similarly influenced habitat selection in the breeding and fall/winter seasons with positive effects above a value of 0.75 (Figure 6b). During the summer, sage-grouse selected for moderate sagebrush continuity ($0.4 < \text{CONTIG} < 0.75$) but avoided very contiguous sagebrush (>0.75). That seasonal variation in sagebrush impacts was also somewhat consistent across study areas (Figure 7). Most notably, there was increasing rate of selection in all four study areas during the breeding season at high CONTIG values (>0.75), but strong avoidance of those same areas during summer in three study areas. In the fourth, Panguitch, there was still a peak in selection at around the same CONTIG value, but very weak selection above that.

The effect of topography also varied seasonally. Most notably, during the breeding season sage-grouse selected most for moderately heterogeneous terrain in all study areas but the Bald Hills, while in summer sage-grouse avoided the moderate terrain and selected either very flat or rugged terrain everywhere but in Panguitch (Figure 8). In fall/winter, the peak of selection in each study area was in terrain of low-to-moderate heterogeneity more than either the least or most rugged terrain.

Model performance

Within each study area, the RF models consistently performed well when predicting withheld data measured by each evaluation metric (Table 3). The TSS for RF models ranged from 0.579 to 0.767 indicating fairly strong predictive performance (Landis & Koch, 1977). Model sensitivity values (proportion of true locations correctly predicted) were also high, ranging from 0.811 to 0.966. The RF models consistently performed better than the RSF models when

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TABLE 3 Random forest (RF) model performance measured by true skill statistic (TSS), proportion of used points correctly predicted (sensitivity), and used-habitat calibration correlation in each study area and each season.

Study area	Season	TSS	Sensitivity	Calibration Pearson's *r*
All	All	0.579	0.806	0.867
All	Fall/winter	0.635	0.846	0.871
All	Breeding	0.604	0.818	0.849
All	Summer	0.589	0.804	0.881
Bald Hills	All	0.707	0.842	0.890
Bald Hills	Fall/winter	0.767	0.952	0.924
Bald Hills	Breeding	0.719	0.966	0.934
Bald Hills	Summer	0.720	0.934	0.912
Cave	All	0.594	0.811	0.804
Cave	Fall/winter	0.642	0.884	0.867
Cave	Breeding	0.638	0.871	0.817
Cave	Summer	0.629	0.855	0.811
Hamlin	All	0.586	0.826	0.886
Hamlin	Fall/winter	0.621	0.861	0.897
Hamlin	Breeding	0.648	0.849	0.892
Hamlin	Summer	0.610	0.825	0.906
Panguitch	All	0.595	0.834	0.873
Panguitch	Fall/winter	0.603	0.844	0.885
Panguitch	Breeding	0.655	0.863	0.916
Panguitch	Summer	0.700	0.835	0.905

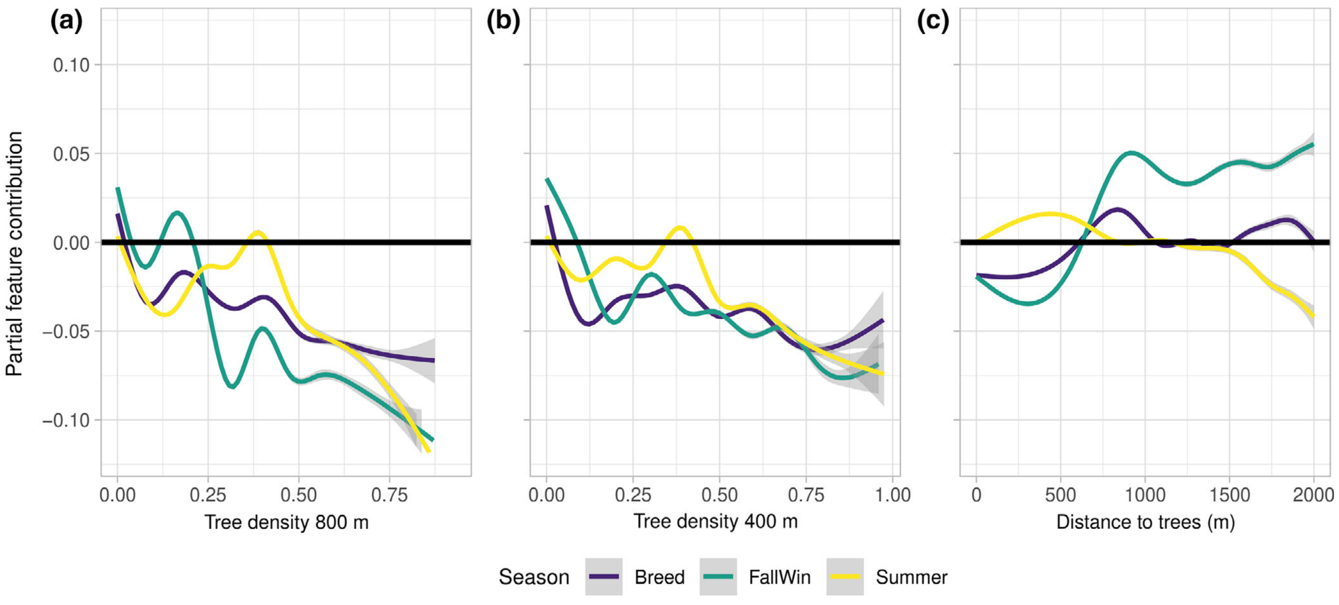

FIGURE 5 Feature contribution to model results in each season of (a) density of treed pixels within 800 m (TREEDEN800), (b) density of treed pixels within 400 m, and (c) distance to trees (TREEDIST).

predicting withheld data and predicting data from other study areas. The RSF models were weaker predictors though still somewhat informative, with TSS values from 0.229 to 0.431 and sensitivity from 0.668 to 0.782.

Used-habitat model calibration also demonstrated moderate to strong model predictive performance (Table 3). The lowest calibration correlation coefficient among all study area–season model combinations

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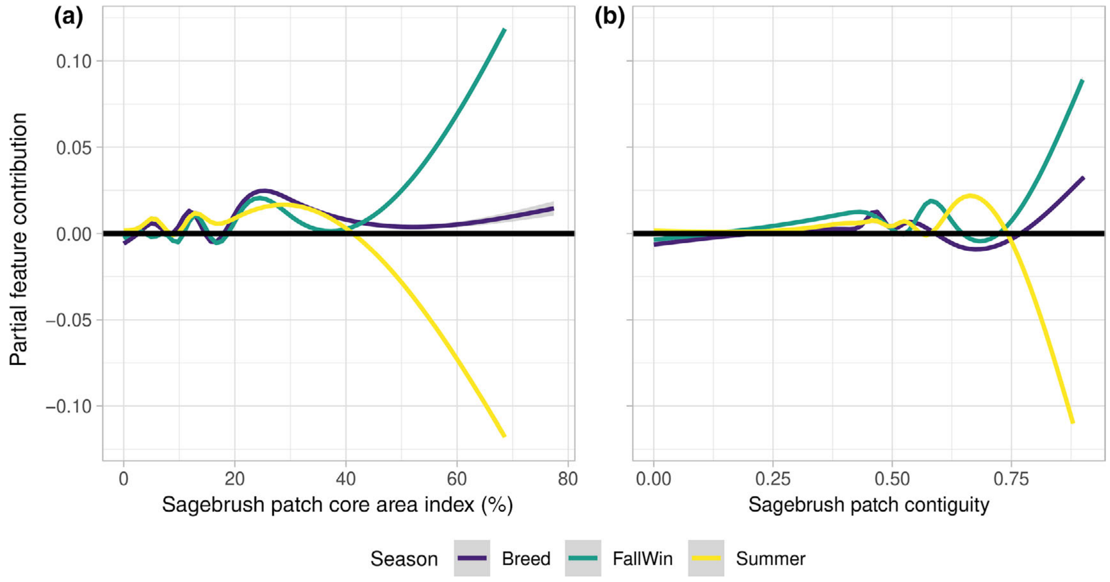

FIGURE 6 Feature contribution to model results in each season of (a) sagebrush core area index (CAI) and (b) sagebrush patch contiguity (CONTIG).

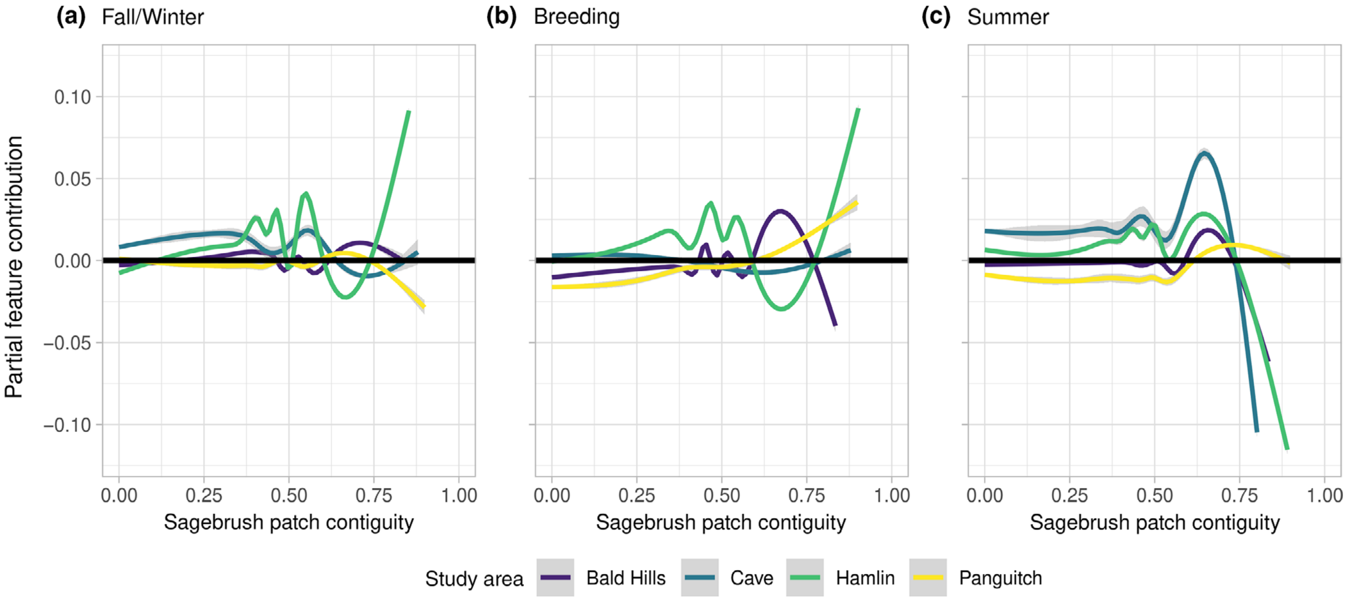

FIGURE 7 Feature contribution to model results in each study area and season of sagebrush patch contiguity (CONTIG).

was in Cave Valley in summer, with an average correlation across iterations of 0.811, while the highest was in the Bald Hills in the breeding season at 0.934.

DISCUSSION

Model performance

The RF models performed very well within study areas and even the model including all study areas and seasons had strong predictive power (TSS = 0.579). The RF model including all study areas was not as accurate as any single study area–season combination model (TSS range = 0.603–0.767; sensitivity range = 0.825–0.966), though the most important variables in each study area were similar. Distance to trees or tree density within 800 m was always among the most important, as was THI400, one of the factors that likely moderates the impact of predation risk due to trees. The failings in predictive power across study areas may derive from a difference in the magnitude and thresholds of the driving variables. For example,

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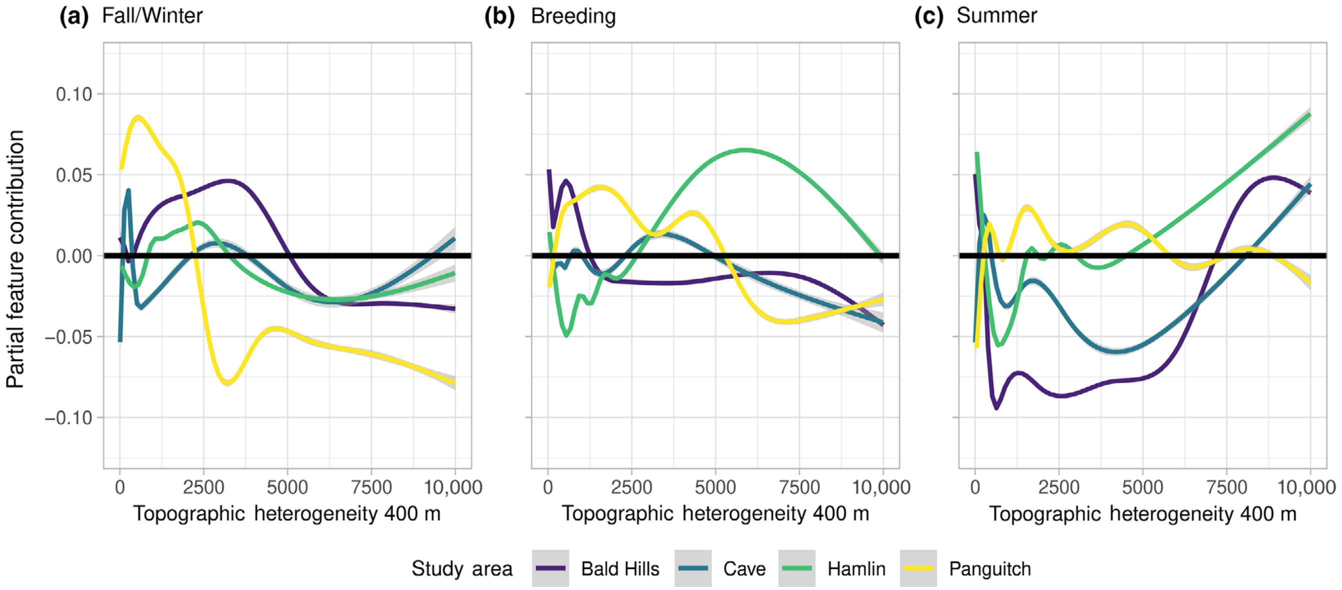

FIGURE 8 Feature contribution to model results in each study area and season of topographic heterogeneity index within 400 m (THI400).

increasing TREEDEN400 in every study area had a generally negative effect on selection, though nonlinearly and with different local perturbations.

We evaluated factors influencing habitat selection at a local scale to determine site-specific selection criteria. In our study region, sage-grouse were more likely to use moderately heterogeneous terrain, small ravines (negative TPI), and larger and more contiguous sagebrush patches compared with available habitat. Similar to past studies, sage-grouse selected lower tree density but did not wholly avoid them (Baruch-Mordo et al., 2013; Doherty et al., 2008; Knick et al., 2013); our analysis suggests that topographical heterogeneity and topographical position in the landscape may moderate the negative impacts of being close to trees suggested by past studies, such as avian predation (Coates et al., 2017; Prochazka et al., 2017). This may be because the topographic features block predator sightlines and make foraging by predators more difficult. Dinkins et al. (2014) found that rugged topography moderated the predation risk posed by golden eagles and proposed that the rugged topography limited the eagles' visual detection of sage-grouse. Our study suggests the same effect through a habitat selection framework. We found that slope was often an important variable, as reported in prior research (Knick et al., 2013). However, our results show that topographic position (being high or low on the landscape) and heterogeneity are more important variables, as did Walker et al. (2016). While slope may be a useful metric, sage-grouse likely select habitat based on the shelter the landscape provides, not its steepness directly. Further, the variable and nonlinear responses suggest that sage-grouse select topography based on other environmental cues like tree cover. It may be that sage-grouse selection is driven by topography only when it can allow them to exploit necessary seasonal resources and minimize predation risk.

Our results also show that sagebrush cover drives selection, perhaps by providing refuge from predation risk. We found that sage-grouse selected for generally greater sagebrush contiguity and avoided tree cover greater than 4%, similar to thresholds identified previously for selection and lek persistence (Baruch-Mordo et al., 2013; Sandford et al., 2017). At any distance from trees, sage-grouse were more likely to select areas of high sagebrush patch contiguity and core area than small and fragmented patches, showing the probable benefit of habitat treatments to remove encroaching conifers.

Regional variation

Our findings reinforce the fact that range-wide predictions must account for regional and local drivers of habitat selection. The results of our study suggest that sage-grouse experience different limitations and drivers of habitat selection throughout their range; across this southern range margin topography plays a stronger role than previously described for any part of their range. In more contiguous sagebrush semidesert or sagebrush steppe habitat, topography was less influential than demonstrated in this study (Doherty et al., 2008; Knick et al., 2013), similar to the findings of Walker et al. (2016), who documented sage-grouse selection

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for somewhat rugged terrain in a naturally fragmented area, especially in winter. Doherty et al. (2016) showed that the most important ecological variables were markedly different across regional sage-grouse management zones. In our study, we worked within only one management zone and further demonstrated the "idiosyncrasies of place" (Jeffress et al., 2013) that are important to evaluate at several scales. We suspect that in areas of sage-grouse range where conifer encroachment is less pervasive, sage-grouse are less likely to exploit topography for shelter from predation.

The place-based RF models for each study area were only moderately informative when predicting the data in the other three study areas. This suggests that sage-grouse make different selection decisions in each study area based on available habitat and limiting factors. It is important to note that we do not believe this is the result of overfitting. Our models consistently outperformed RSFs, despite our measures to avoid overfitting restricting to some extent the ability of the RF models to describe idiosyncrasies and interactions. Through increasing minimum node size and using a repeated LGOCV, we decreased the risk of any group of individuals or spatial cluster excessively contributing to model development and driving overfitting. These results strengthen the argument for place-based planning and conservation (Doherty et al., 2016; Picardi et al., 2020). The regional variation in selection detected by our study suggests that while models at the range-wide or state-wide scale have great utility for general understanding, predictions and planning should be based at local or regional scales whenever possible.

Our results further support existing findings about the impacts of conifer encroachment and the utility of conifer removal, but also point to the need for place-based conservation and management planning and action (Coates et al., 2020; Frey et al., 2013; Picardi et al., 2020; Sandford et al., 2017). Based on our findings of where sage-grouse select habitat close to trees, conifer removals may be most effective in areas where grouse lack other shelter (from topography or largely contiguous sagebrush) to reduce predation risk. We found that sage-grouse select relatively flat topography in some cases and some parts of the year, and it is likely that they face some trade-offs in using more rugged terrain. Given that sage-grouse are not large animals and much of the predation risk they apparently react to is due to fairly short trees, topography likely does not need to be extremely rugged to provide shelter. This should inform understanding of local habitat conditions in different areas of sage-grouse distribution. Statewide or regional models will be most useful for tracking general population trends and habitat loss to identify the areas of sage-grouse range most in need of conservation effort or further research.

Seasonality

Many previous studies have found seasonal variation in sage-grouse habitat requirements. Our data support these past studies; within any study area or across all four, the greatest predictive performance was in models of one season rather than the whole year. Our study reaffirms some of the seasonal components to selection previously described, including a greater affinity for large areas of sagebrush and generally less heterogeneous terrain in winter than in summer (Carpenter et al., 2010; Doherty et al., 2008). However, the effect was nonlinear, and sage-grouse during summer in all four study areas and during fall/winter in all but Hamlin avoided the most contiguous sagebrush patches (Figure 8), which may offer inadequate thermal cover or food resources during these times. We found that as distances farther than 1000 m from trees, sage-grouse selection became less likely during summer, and in each study area, there was a generally decreasing probability of selection with increasing distance to trees. This may be because in our relatively xeric study areas, mesic resources necessary to survive the summer (Drut et al., 1994) are less likely to be found where there is too little water for trees to persist (West, 1983a). It may also be that sage-grouse along this southern range margin use areas with trees in summer as thermal cover, despite the predation risk, especially when they can also exploit topography for visual cover, as we found that selection during summer for the most rugged terrain tended to be higher than for moderately heterogeneous terrain.

CONCLUSIONS

Our findings support the need for conservation at multiple scales, especially as climate change and increasing habitat fragmentation force species redistributions and extirpations (I.-C. Chen et al., 2011; Mosblech et al., 2011). For sage-grouse, this means taking into account the considerable variation in habitat conditions and requirements across their range at both regional and local scales (Dahlgren et al., 2019; Doherty et al., 2016; Picardi et al., 2020). To create more suitable habitat, management actions should identify the local limitations in addition to macroecological drivers. At the southern range margin, our findings support focusing conifer removals in areas with little cover from heterogeneous topography or contiguous sagebrush and where the removal will foster greater, essential sagebrush connectivity (Connelly et al., 2000; Wisdom et al., 2005).

Sage-grouse exhibit site fidelity, and individuals may be unlikely to seek better habitat as the southern range

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margin is pushed northward (Baxter et al., 2008; Doherty et al., 2010; Dunn & Braun, 1985; Fischer et al., 1993). Range shifts will therefore be forced largely by extirpation, not individual responses, especially in combination with decreasing habitat quality and connectivity along a potential range shift path. Sagebrush habitat itself is likely to become patchier and less productive at its southern range margin in response to climate change, but may in fact increase in cover in cooler areas of its range (Kleinhesselink & Adler, 2018; Renwick et al., 2018). Sage-grouse response to landscape change will likewise be heterogeneous, and place-based models and monitoring will be crucial to understanding how they adapt to newly available habitat or fail to do so (e.g., to habitat created by large-scale removal of encroaching conifers). Sage-grouse reliance on sagebrush for both food and cover means that as sagebrush cover declines and pinyon–juniper encroachment continues, sage-grouse will likely be extirpated from southern areas of their range as they lose important food resources and refuge from predation. While sage-grouse are a clear example of variation in species' habitat requirements at various scales, this also applies to many other species potentially threatened by landscape changes and fragmentation. Examining habitat suitability variation along the range margin will be a critical step to inform a more nuanced understanding for conservation and management of threatened species.

ACKNOWLEDGMENTS

We acknowledge and thank our many partners and colleagues who assisted in this work. Our research was supported by grants from the Alton Coal, LLC, US Department of the Interior Bureau of Land Management, and the Nevada Department of Wildlife. For assistance in data management and sage-grouse capture efforts, we thank Moira Kolada, Shawn Espinosa, Curt Baughman, Kody Menghini, Chelsea Wisner, Sarah McNamara, Ben Donnelly, Erica Hansen, and all other volunteers who generously gave their time.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data on sage-grouse locations are sensitive, concerning a threatened species, owned by state agencies, used through a memorandum of understanding, and cannot be provided here. Others interested in using those data may request them from the Utah Division of Wildlife Resources with a Government Records Access and Management Act request and from Nevada using a Nevada Department of Wildlife public records request. The LANDFIRE data may be accessed through landfire.gov. Elevation data were sourced using the *elevatr* R package from https://registry.opendata.aws/terrain-tiles/. We downloaded LANDFIRE and elevation data over the spatial extent of our study areas with a 1-km buffer around each side.

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How to cite this article: Beers, Aidan T., and Shandra N. Frey. 2022. “Greater Sage-Grouse Habitat Selection Varies across the Marginal Habitat of Its Lagging Range Margin.” *Ecosphere* 13(7): e4146. https://doi.org/10.1002/ecs2.4146

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