

Greater sage-grouse face tradeoffs between predation risk and thermal exposure in selecting habitat

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August 2, 2023

Abstract

Climate change is likely to drive widespread species range shifts and extirpations, mostly on the warm distribution edges, where habitat tends to be fragmented, of lower quality, support lower population density, and at greater risk from extreme weather events. In the Intermountain West, future climate will likely be warmer and drier, driving a reduction in sagebrush (*Artemisia* sp.) and other shrubland cover. Among the species threatened by more xeric climate is the Greater sage-grouse (*Centrocercus urophasianus*), which depends on sagebrush for forage and shelter, though their response to temperature is not well studied. We deployed 75 data loggers across two valleys in southern Utah and Nevada, near the southern edge of sage-grouse distribution, and collected temperature data for 27 months. We used random forest models to test the impacts of temperature, land cover, and topography on sage-grouse habitat selection and found that temperature influenced selection in all seasons and both sites. In Utah, the warmer site, sage-grouse selected areas near trees during the extremes of both winter and summer. In autumn and spring those extremes were rarer and sage-grouse avoided habitat near trees. Conversely, sage-grouse in the cooler Nevada site selected contiguous patches of sagebrush in extremes periods but only selected habitat near trees during winter cold, avoiding trees during summer. Our findings show that extreme temperatures drive sage-grouse to select habitat near trees despite the risk likely posed by avian predators. The difference between the Utah and Nevada sites suggests that sage-grouse prefer sagebrush as thermal shelter but that it may be inadequate during the hottest times, forcing riskier selection. These models point toward a more mechanistic understanding of how sage-grouse distribution may retract at its warm edges. This will refine our understanding of seasonal habitat requirements and inform management decisions to prioritize thermal refugia for an imperiled species.

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ABSTRACT

Climate change is likely to drive widespread species range shifts and extirpations, mostly on the warm distribution edges, where habitat tends to be fragmented, of lower quality, support lower population density, and at greater risk from extreme weather events. In the Intermountain West, future climate will likely be warmer and drier, driving a reduction in sagebrush (*Artemisia* sp.) and other shrubland cover. Among the species threatened by more xeric climate is the Greater sage-grouse (*Centrocercus urophasianus*), which depends on sagebrush for forage and shelter, though their response to temperature is not well studied. We deployed

75 data loggers across two valleys in southern Utah and Nevada, near the southern edge of sage-grouse distribution, and collected temperature data for 27 months. We used random forest models to test the impacts of temperature, land cover, and topography on sage-grouse habitat selection and found that temperature influenced selection in all seasons and both sites. In Utah, the warmer site, sage-grouse selected areas near trees during the extremes of both winter and summer. In autumn and spring those extremes were rarer and sage-grouse avoided habitat near trees. Conversely, sage-grouse in the cooler Nevada site selected contiguous patches of sagebrush in extremes periods but only selected habitat near trees during winter cold, avoiding trees during summer. Our findings show that extreme temperatures drive sage-grouse to select habitat near trees despite the risk likely posed by avian predators. The difference between the Utah and Nevada sites suggests that sage-grouse prefer sagebrush as thermal shelter but that it may be inadequate during the hottest times, forcing riskier selection. These models point toward a more mechanistic understanding of how sage-grouse distribution may retract at its warm edges. This will refine our understanding of seasonal habitat requirements and inform management decisions to prioritize thermal refugia for an imperiled species.

KEYWORDS: greater sage-grouse, habitat selection, thermal ecology, Basin and Range, random forest, range margins, *Centrocercus urophasianus*

COVER LETTER:

Allen Moore, Andrew Beckerman, Chris Foote, Gareth Jenkins, Marcus Lashley, and Zhaoxue Ma

Editors-in-chief

Ecology and Evolution

Dear Editors,

We are very pleased to submit our article, *Greater sage-grouse face tradeoffs between predation risk and thermal exposure in selecting habitat*, for consideration at *Ecology and Evolution*.

In this research, we used GPS transmitters to track the habitat selection of greater sage-grouse in the fragmented habitat of their southern range margin. As sagebrush habitat specialists, greater sage-grouse are more vulnerable to predation in areas of greater habitat fragmentation. It is clear that encroaching conifer forests provide perches for avian predators and threaten sage-grouse habitat, and previous research suggests that sage-grouse select more rugged terrain when near trees. However, it is unclear what may compel sage-grouse to select habitat near trees rather than avoiding them altogether. Here, we present evidence that along their southern range margin, greater sage-grouse may be forced by high temperatures to seek thermal refuge in tree cover when sagebrush is inadequate shelter. This has important implications for how we understand the risks faced by this imperiled species and the factors land managers must consider for their conservation, especially in the face of ongoing climate change.

We believe that *Ecology and Evolution* would be an excellent means to disseminate our research. Sage-grouse are a species of conservation concern that may serve as an indicator species for sagebrush ecosystems and the challenges they face are emblematic of those faced by other habitat specialists and of conservation efforts in general.

We declare no conflicts of interest and would be happy to correspond further at aidan.beers@montana.edu or aidantb@gmail.com.

Thank you for your time and consideration.

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INTRODUCTION

Ongoing climate change is forcing species redistributions and local extirpations, driving shifts in habitat suitability and connectivity and compelling wildlife to shift their range or modify their behavior to avoid extirpation (Thomas et al. 2004a, Parmesan 2006, Chen et al. 2011b, Varner et al. 2016, Beever et al. 2017, Pecl et al. 2017). However, the rates of change in habitat suitability are heterogeneous across a species' range, as climate is not always the dominant driver of range limits (Arntzen and Espregueira Themudo 2008, Balzotti et al. 2016, Oldfather et al. 2020). Habitat fragmentation (sometimes as an effect of climate) has been implicated as a primary driver that both has direct effects and can exacerbate the impacts of climate (Opdam and Wascher 2004). Furthermore, local- and micro-scale climates can be decoupled from regional trends, especially by topography, complicating predictions of population persistence and connectivity (Dobrowski 2011, Ashcroft et al. 2012, Gollan et al. 2015). That decoupling can create microrefugia (Rull 2009, Hannah et al. 2014) where suitable habitat persists longer than expected at macroecological scales. This complicates and can limit our understanding of how species and ecosystems will respond to climate change and can reduce the capacity to plan for and manage change for sensitive species.

Microrefugia and their impact on species are especially important at species' lagging range margin, where habitat is likely to be fragmented and of lower quality. Even for mobile wildlife species, suitable microhabitat can provide essential refuge from thermal stress and extreme events that otherwise drive local extirpations at range margins (Parmesan 2006, Seabrook et al. 2014, Lima et al. 2016). For species of conservation concern, studying their limiting factors at range margins can provide insight into their capacity to shift their range or behaviorally adapt to new conditions. In particular, the lagging range margin can be used as a natural laboratory to evaluate the environmental factors limiting the defining range limits and portend the conditions likely to become more common at their current range core (Travis and Dytham 2004, Keith et al. 2008, Seabrook et al. 2014). It is therefore critical to identify the mechanisms limiting habitat suitability for sensitive species at their lagging range margin at multiple scales (Vale et al. 2014).

Large-scale patterns in species distribution often do not scale down and can neglect variation in habitat suitability at finer scales, especially at range margins where species distribution models (SDMs) tend to be less accurate (Hannah et al. 2014, Vale et al. 2014). While much of the research on range limitations focuses on occupancy, studying wildlife habitat selection may offer further insight into how individuals are compelled to exploit microhabitat in response to thermal stress. Shifts in wildlife behavior in response to thermal stress or other climatic drivers often precede detectable shifts in distribution or population processes (Berger-Tal et al. 2011, Beever et al. 2017). By focusing on tendencies in individual habitat selection, we are able to identify the environmental factors that foster suitable microhabitat and better inform management at local scales for sensitive species. In combination with large scale distributions, understanding limits on habitat selection at range margins can provide more accurate estimates of wildlife response and sensitivity to climate change.

The range of sagebrush of western North America has declined rapidly due primarily to land conversion, improper grazing management, fire, invasive species, and loss to grassland and forest (Connelly and Braun 1997, Connelly et al. 2004). Sagebrush species (*Artemisia sp.*) will likely have varied responses to ongoing

climate change, but at their southern range limit they are likely to decrease in cover in response to climate warming (Tredennick et al. 2016, Kleinhesselink and Adler 2018, Renwick et al. 2018).

As a sagebrush obligate, greater sage-grouse (*Centrocercus urophasianus*, hereafter “sage-grouse”) range has declined in response to loss of sagebrush-dominated habitats (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004). Sage-grouse are a species of conservation concern emblematic of the sagebrush system and may serve as an indicator of ecosystem change there (Rowland et al. 2006, Hanser and Knick 2011, Runge et al. 2019, Ricca and Coates 2020). Habitat specialists like sage-grouse are less able to adapt to novel conditions (Hampe and Petit 2005), so studying their habitat selection along their lagging (southern) range margin provides an opportunity to assess the factors likely to limit suitable habitat and portend future changes to their distribution and to sagebrush habitats.

For sage-grouse, it is clear that sagebrush extent is an essential driver of their habitat, but it is not the only limitation, as sagebrush range extends far south of that of sage-grouse. So while SDMs for sage-grouse likely explicitly include sagebrush (Balzotti et al. 2016), a habitat selection framework can elucidate important points of stress and cryptic fragmentation that would be overlooked at coarser scales or by focusing on occupancy. In particular, it is important to assess the effects of direct thermal stress on selection, as extreme weather could preclude using otherwise suitable habitat. While other gallinaceous birds are sensitive to temperature (Patten et al. 2007, Hovick et al. 2014, Londe et al. 2021), thermal effects on sage-grouse are not clear. Pratt et al. (2017) used relatively coarse scale PRISM data (4 km resolution: [PRISM Climate Group 2020]) to study the role of temperature in triggering sage-grouse seasonal migration; that study indicated sage-grouse make coarse scale decisions about their habitat in response to temperature, but it did not address the degree to which sage-grouse select habitat within seasons in response to thermal stress or how seemingly intact habitat can be or will become untenable due to temperature.

In addition to sagebrush extent, sage-grouse habitat selection and long-term persistence is strongly impacted by tree cover, especially encroaching forests of pinyon pine (*Pinus monophylla* and *P. edulis*) and juniper (*Juniperus spp.*), as conifers can replace sagebrush cover and may provide perches for avian predators (Frey et al. 2013, Prochazka et al. 2017, Severson et al. 2017b, 2017a, Olsen et al. 2021). Large-scale studies of sage-grouse lek persistence and population trends suggest that tree cover can be among the greatest threats to sage-grouse and other sagebrush obligates (Davies et al. 2011, Baruch-Mordo et al. 2013, Knick et al. 2013), though to our knowledge only one study has directly linked conifer cover with decreased survival (Prochazka et al. 2017). Yet despite the poorer habitat quality and likely risk of avian predators, sage-grouse sometimes select habitat near trees, possibly mitigating that risk by exploiting rugged topography to block predator sightlines (Dinkins et al. 2014, Beers and Frey 2022a). The reason for this apparent incongruity between some observed selection and population processes is unclear. However, it has been suggested that sage-grouse may be prone to ecological traps or maladaptive selection, wherein they select areas of greater risk to exploit its resources in spite of negative fitness impacts (Kirol et al. 2015, Coates et al. 2017, Pratt and Beck 2021). The reasons for that potentially risky selection have not been explored.

It is likely that sage-grouse will be extirpated from large swathes of their current southern range if warming and drying trends continue, resulting in sagebrush conversion to grassland, increased fire frequency, and decreased soil moisture and mesic resources (Schlaepfer et al. 2012a, Kleinhesselink and Adler 2018). To best conserve sage-grouse, it is therefore important to assess the role that thermal stress plays in driving their habitat selection in the fragmented habitat of their southern range edge. In identifying the direct impact of temperature on selection, we will be better able to predict the local and regional variation in habitat suitability along the lagging range margin and to inform conservation efforts to foster potential microrefugia. Knowledge of selection for suitable microhabitat can complement larger scale efforts and inform ecosystem management to better identify areas at multiple scales that are most likely to support that microhabitat and to take actions to foster or create it (Kirol et al. 2015).

In this study, we sought to identify trends in sage-grouse habitat selection within each season in response to near-surface temperature, to determine when and where sage-grouse select habitat in response to temperature and identify where temperature is most likely to limit habitat suitability. We hypothesized that sage-grouse

would make micro-scale habitat selection in response to extreme temperatures within their home range and within otherwise suitable sagebrush habitat.

MATERIALS AND METHODS

Study areas

We performed this study in two valleys near the sage-grouse southern range margin. Both valleys were a mosaic of sagebrush and grasses bordered by mountains (Figure 1). In this region sagebrush is largely *Artemisia tridentata wyomingensis* with patches of other *A. tridentata* subspecies and some patches of *A. nova* in the more xeric areas. The mountainous areas included some patches of sagebrush, but were largely dominated by mixed pinyon-juniper forest (*P. monophylla* and *J. osteosperma*), mountain mahogany (*Cercocarpus sp.*), and occasional stands of aspen (*Populus tremuloides*). In each valley, the pinyon-juniper forest was expanding farther into the valley, and in each there had been management actions to remove some of that expansion.

Buckskin Valley and Bear Valleys in Utah are in the Panguitch Sage-grouse Management Area (SGMA; Utah Public Lands Policy Coordination Office 2019). This Bear-Buckskin complex (hereafter, Buckskin) was the smaller of the two study areas (~220 km²), located farther south, and had a smaller elevation range used by sage-grouse (2100 – 2500 m). The highest areas were the ridge between the two valleys and the lowest was the open, flat center of Buckskin Valley. There were large patches of dense sagebrush as well as large extents with little to no sagebrush, which was covered by grasses (annuals and native bunchgrasses) and bare ground. Over the 30-year period (1991 – 2020) used to define PRISM data climate normal, Buckskin had a mean annual temperature of 7.3 °C and received 435 mm of precipitation. A large portion of that precipitation (127mm) came during the spring, March – May, though the second-wettest month on average was August and the second-wettest three-month period was December – February (109 mm). There was a mean monthly difference in maximum and minimum temperatures of 18.1 °C. During the study period, Buckskin had a mean annual temperature of 8.6 °C and an average of 345 mm of precipitation each year. The hottest month was August ($T_{\text{mean}} = 19.8$ °C) and the coldest was February ($T_{\text{mean}} = -3.9$ °C). There was a mean monthly difference between maximum and minimum temperatures of 15.2 °C. The northern half of Buckskin is divided by Utah State Highway 20, which sees moderate traffic. Bear Valley had a few small houses and ranch buildings, but there were none in Buckskin. Buckskin and Bear Valleys each had a few small gravel roads through them.

Steptoe Valley is part of the Steptoe/Cave Population Management Unit in Nevada (Emm et al. 2019). It is larger than Buckskin (~540 km²) and is interspersed with patches of grasslands throughout the valley, commonly including cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), Sandberg’s bluegrass (*Poa secunda* or *Poa sandbergii*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and Indian ricegrass (*Oryzopsis hymenoides*). Within this study area, grouse were generally located at higher elevations than in Buckskin, Utah (2000 – 2700 m). Buckskin had a greater seasonality in its precipitation and tended to be warmer than Steptoe in each of their respective wettest and driest quarters of the year.

Compared to Buckskin, Steptoe was drier and of about the same temperature across the entire year, despite have less seasonality. From 1981 – 2010, Steptoe had a mean annual temperature of 7.3 °C and 317 mm of annual precipitation. Like in Buckskin, most of the precipitation fell in March – May (87 mm) and the second wettest quarter was December - February (78 mm). In Steptoe, the warmest month (July) had an average maximum temperature of 30.3 °C and the coldest month (December) an average minimum temperature of -11.1 °C. There was a mean monthly difference in maximum and minimum temperatures of 18.1 °C. During the study period, Steptoe received an average of 233 mm of precipitation. The hottest month was July ($T_{\text{mean}} = 19.6$ °C) and the coldest was February ($T_{\text{mean}} = -3.9$ °C). During the study period there was a mean monthly difference in maximum and minimum temperatures of 19.3 °C. In Steptoe, there was a dirt road on either side of the valley and the two met where the low area of the valley narrowed to about 3 km across. Where the valley is close to 10 – 12 km across, there are a few permanent structures on the west side,

mostly clustered together. There is also a small state park, Ward Charcoal Ovens State Historic Park, near the edge of the treeline with several stone charcoal ovens. Like much of sage-grouse habitat in the Great Basin, both Buckskin and Steptoe are used for cattle ranching and sage-grouse could encounter both cattle and cattle-grazed habitat in almost any part of each study area.

Landscape covariate data

We downloaded 30 m resolution land cover data from the Landscape Fire and Resource Management Planning Tools Project database (LANDFIRE; Rollins 2009) to build rasters of cover by sagebrush and trees. We first generalized the land cover types, reclassifying all cover types that included the words “tree,” “woodland”, “forest”, “conifer”, and “juniper” as tree cover, and any type described as “sagebrush” or “*Artemesia*” as sagebrush cover. We created metrics of tree cover—the density of “tree” pixels within 400 m and 800 m radii (TREEDEN400 and TREEDEN800) and the distance to any “tree” pixel (TREEDIST). Because the size and configuration of sagebrush patches can be important for sage-grouse survival, we used the *landscapemetrics* package in R (Hesselbarth et al. 2019) to calculate the contiguity (CONTIG) and core area index (CAI) of sagebrush patches. Pixels that fell outside of sagebrush cover received a score of 0 for each of those metrics. CONTIG measures the degree to which pixels within a patch of a single cover type are connected and values can range from zero to one. CAI measures the percentage of pixels of cover type patch that are not adjacent to pixels of a different cover type. As a patch increases in size and interior area, CAI approaches 100.

Because topography plays a role in sage-grouse survival and habitat selection (Aldridge et al. 2008, Knick et al. 2013, Dinkins et al. 2014, Picardi et al. 2020, Beers and Frey 2022a), We also included metrics of topographic position and heterogeneity. We first used the R package *elevatr* (Hollister et al. 2017) to download a 10 m resolution digital elevation model (DEM) for each study area, then used that DEM to calculate indices of topographic position (TPI) and heterogeneity (THI) within moving window sizes of 50 m, 200 m, and 400 m. TPI (Jenness et al. 2013) is a measure of how high or low any DEM cell is compared to the cells around it within a user-defined radius. Cells with negative values are lower than the terrain around them and positive values indicate a high point or ridge. THI is a measure of overall ruggedness, calculated by summing the absolute value of TPI at every cell within moving window sizes of 50 m, 200 m, and 400 m.

Temperature data

We deployed HOBO Pendant Temperature/Light data loggers (Onset Corporation, Bourn, MA, USA, #UA-002-64) in a stratified random distribution in each valley, placed within areas of known sage-grouse use, collecting data every 30 minutes from June 2018 – November 2020. We attached the loggers to sagebrush or other shrubs where available to minimize exposure to direct sunlight, on the north side of the shrub. At points where there was no shrub available, we attached the logger to an aluminum tent stake and drove it into the ground on the north side of a bunchgrass. At each type of location, we positioned the logger 15 – 25 cm above the ground to mimic the conditions a sage-grouse would experience.

In July 2019 we picked up the loggers to download the data, install a new battery, and redeploy them in a different random configuration. In both years some of these loggers failed or were destroyed (seemingly by cows, ravens, and coyotes). Of the loggers deployed in 2018, we were able to use data from 31 from Steptoe and 22 Buckskin. Of those deployed in 2019, we used data from 40 loggers from Steptoe and 28 loggers from Buckskin. For each logger, we excluded any data where light intensity was $> 10,000$ lumens to exclude warming from direct sunlight. This filtering left a total of 1,016,833 data points. In combination with loggers lost to extreme cold and animals, data omitted due to direct sunlight, and the loggers being deployed in summer, in both Buckskin and Steptoe we had the most temperature data points in Autumn (Buckskin $n = 100,362$; Steptoe $n = 168,901$), followed by Summer (Buckskin $n = 94,264$; Steptoe $n = 156,610$), Winter (Buckskin $n = 66,914$; Steptoe $n = 112,597$), and Spring (Buckskin $n = 56,816$; Steptoe $n = 95,823$). From those points, we pulled the daily maximum, minimum, and difference (T_{\max} , T_{\min} , T_{diff} , respectively) and then calculated the monthly average for each of those metrics for each logger.

After calculating the T_{\max} , T_{\min} , and T_{diff} for each logger and each month in the study period, we created

an interpolated surface at a 100 m resolution and aggregated the monthly averages by season. We performed the interpolation using the interpolation tools in ArcMap version 10.6 (Environmental Science Research Institute (ESRI), Inc., Redlands, California, USA), co-kriging across the extent of the study area in each valley assuming that temperature varied with elevation. While elevation is not the only driver of temperature at local scales, it is an important factor (Dobrowski 2011, Ashcroft and Gollan 2012), thus we did not include a separate measure of elevation in the habitat selection analysis to avoid problems of variable collinearity. We grouped September – November as Autumn, December – February as Winter, March – May as Spring, and June – August as Summer.

GPS data

For sage-grouse locations, we tracked individual birds using rump-mounted GPS transmitters (22 g Solar Argos/GPS PTT-100, Microwave Telemetry Inc., Columbia, MD; 22 g GPS-PTT, GeoTrak, Inc., Apex, NC). We captured sage-grouse at night with little to no moon illumination using spotlights and dip nets, searching on foot in groups of 2 – 4 in areas of known or suspected sage-grouse use (after Giesen et al. 1982). While handling the sage-grouse, we assessed their age, sex, mass, and body condition. We declined to put a transmitter on any grouse with an injury or a mass less than 1 kg. We released grouse at the capture site and monitored their departure flight to ensure that bird was moving naturally. The sage-grouse included in this study were captured in years 2017-2019. This research protocol was reviewed and approved by the Utah State University IACUC (#10175, #11161).

The GPS transmitters logged four locations per day. For this study, we removed from the dataset any points from within 48 hours of a sage-grouse’s capture date, points for any grouse with fewer than 100 successful GPS fixes, and points that fell outside of the spatial extent of the data loggers in each study area or outside the study period of June 2018 – November 2020. This left a total of 8163 data points from 14 birds in Buckskin and 7209 locations from 15 birds in Steptoe. We calculated a 90% home range for each sage-grouse from a kernel density estimator using the R package *adehabitatHR* (Calenge 2017). Within that home range, we randomly generated points to sample the landscape as “available habitat” at a 1:10 ratio in a used-available design (Johnson 1980, McDonald et al. 2013). However, for each run of the models we randomly selected from within the available habitat point dataset for a 1:1 ratio between used GPS detection points and available habitat sampling points. This 1:1 ratio avoids problems that can arise from oversampling from one class of the response variable in a classification method like random forest classification (Chen et al. 2004, MacKenzie 2005, Reisinger et al. 2021, but see Street et al. 2021).

Model Construction

We grouped the data within the two study areas and within four seasons, creating eight groups of data for analysis. For each of those data groups, we built models both including and excluding temperature to assess how temperature affected model performance, analogous to using a null model for comparison. For each analysis, we built random forests (RF) (Breiman 2001), a simple machine learning algorithm that has been used successfully with complex ecological datasets (De’ath 2007, Yu et al. 2020), including presence-only and animal habitat selection data (McDonald et al. 2013, Mi et al. 2017, Zhang et al. 2019, Picardi et al. 2020, Rather et al. 2020). RF is a tree-based classification model that uses a bootstrap sample of the data provided to train a model and a withheld sample to test each iteration of the tree. It has outperformed a traditional logistic regression approach in a used-available framework, including wildlife habitat selection (Cushman et al. 2010, Mi et al. 2017, Cushman and Wasserman 2018, Shoemaker et al. 2018, Rather et al. 2020). We used the R packages *ranger* (Wright et al. 2021) and *caret* (Kuhn 2016) to grow the RF with a leave-group-out cross validation (LGOCV) grouped by sage-grouse ID to build these models. We used 70% of the data for initial model training with a random subset of 30% of the data withheld for model validation. We tuned the models in the training process by allowing the number of features selected for testing at each node (*mtry*) to vary between 2, 3, 4, 5, 8, and 10. To minimize the chance of overfitting, we also set the minimum node size at 50 points, which prevents each decision tree in the model from making inferences on too little data (Valavi et al. 2021).

To evaluate each model’s performance, we used the *caret* package (Kuhn 2016) in R to predict the withheld 30% of the data and measured model performance by the true skill statistic (TSS), Cohen’s kappa, model sensitivity, and used-habitat calibration (Fieberg et al. 2018). TSS measures both model specificity and sensitivity while being insensitive to prevalence (Fielding and Bell 1997, Allouche et al. 2006). There is also an argument that model evaluation metrics for presence-background (i.e., used-available) data should not be prevalence-insensitive (Stephanie et al. 2001, Lawson et al. 2014), so we also included Cohen’s kappa in model validation. Kappa ranges from -1 to 1, where higher values indicate greater model performance or strength of agreement between withheld data and the model’s predictions (Cohen 1960). A guideline for evaluating kappa suggests that a range 0.41 – 0.6 suggests “moderate” agreement, 0.61 – 0.80 “substantial” agreement, and 0.81 – 1.00 “almost perfect” agreement (Landis and Koch 1977). The same guideline applies to TSS. Further, because the available points in a used-available design do not necessarily represent species absence, we also calculated the model’s performance in predicting only the true presence points (the model’s sensitivity) and calculated the correlation in used-habitat calibration. We repeated the process of dataset division ten times for each study area and season and report the average model performance metrics.

We also measured variable importance in each model using the mean decrease in Gini node purity (Calle and Urrea 2011), which measures each variable’s contribution to the RF model’s ability to distinguish between response variable classes. We examined the impact of different variables using partial dependence (R package *pdp* : Greenwell 2017), which is useful for interpreting RF models and others modeling methods that measure nonlinear effects (Elith et al. 2008, Robinson et al. 2017). In our models, partial dependence plots visualize the marginal effect of an independent variable on the model’s predicted used vs available outcome at every value of that independent variable when the effects of all other covariates are held at their mean value. Partial dependence plots are also useful for showing the interaction of two variables in predicted selection or avoidance, where two independent variables are on adjacent axes and the dependent variable is represented by a color gradient in the two-dimensional space of the plot.

RESULTS

Temperature data

At a broad spatial scale, the average ambient temperatures of Buckskin and Steptoe were nearly equal, though Steptoe experienced both warmer maximum and colder minimum temperatures while being drier (PRISM Climate Group 2020). However, the data collected from the data loggers indicated that Buckskin was slightly warmer in all four seasons (all t-test $p < 0.001$, Table 1). Buckskin had a higher mean temperature in summer months; Steptoe had a colder mean winter minimum temperature.

Model performance

We generated sixteen different model combinations of study area, season, and data logger temperature inclusion. By comparing the performance of models in the same study area and season with and without temperature metrics, we evaluated the degree to which temperature drives sage-grouse habitat selection in each of those situations. Most study area – season model combinations performed adequately or better, regardless of whether the model included temperature data (Table 2). Here, we report a “mean performance” for each model by averaging the value of each performance metric, which is a simple way to initially describe model performance.

In Buckskin, Utah, all models that included data logger temperature performed moderately to very well, showing “substantial” ($0.61 < \text{kappa} < 0.80$) to “near-perfect” ($\text{kappa} > 0.81$) agreement between training data model predictions and withheld testing data. The best performing model was in Summer, which performed best by all metrics (mean performance = 0.940), followed by Spring (0.840), Winter (0.828), and Autumn (0.825) (Table 2). For each evaluation metric, the Summer model’s performance was in the range of “near perfect” agreement between model predictions and withheld data, and including temperature covariates improved model performance most in Summer (Table 2). The performance of the poorest models that

included temperature still suggest adequate or good performance. When excluding temperature, mean model performance was again highest in Summer (0.856), followed by Winter (0.824), Spring (0.815), and Autumn (0.811). Notably, model performance was slightly higher without temperature covariates than with them by at least one evaluation metric in Winter (sensitivity), Spring (kappa), and Autumn (kappa), suggesting less impact of temperature on selection in those cooler seasons (Table 2).

In Steptoe, Nevada, the best performing model that included temperature covariates was also in Summer (mean performance = 0.815). Mean performance was lower but still good in Spring (0.774), Winter (0.788), and Autumn (0.804). For each seasonal model with temperature covariates, TSS was greater than 0.63, kappa was greater than 0.62, sensitivity was greater than 0.78, and UHC correlation was greater than 0.96 (Table 2). Steptoe models excluding temperature covariates also performed at least moderately well by each evaluation metric, with acceptable mean model performance in Summer (0.746), Winter (0.727), Autumn (0.726), and Spring (0.711). The greatest change in model performance in predicting withheld data due to including temperature was in Autumn (Δ mean model performance = 0.064). The next largest changes in performance due to temperature were in Spring (0.061), Winter (0.056), and Summer (0.058).

By including temperature in Steptoe’s Summer and Winter models, when temperatures were most extreme and therefore most likely to be limiting, model performance improved by model sensitivity = 0.057 and 0.047, respectively. Similarly, the same comparisons in Buckskin showed a change in sensitivity of 0.134 in Summer and -0.037 in Winter due to including temperature in the models. This shows a greater impact of temperature in both study areas during Summer than in Winter. Furthermore, there was a proportionally larger impact in Buckskin than in Steptoe. Including temperature in Buckskin had a greater absolute impact on model sensitivity, and the difference in improvement caused by adding temperature was greater in Buckskin (0.171) than in Steptoe (0.010).

Variable importance

Our RF models of sage-grouse habitat selection showed that temperature metrics played an important role in each model combination of study area and season as measured by the mean decrease in Gini index. Compared to the other variables included, temperature was the most important in Summer in both Steptoe and Buckskin (Table 3). Although of less influence in Winter, temperature variables were still important to model fit. In Buckskin, sagebrush patch contiguity was among the three most important variables in every model whether or not temperature was included. In contrast, sagebrush contiguity was not among the most important variables in Steptoe in any model. Distance to trees (TREEDIST) was more important than sagebrush patch contiguity and core area index in every model. In all seasonal models excluding temperature covariates, distance to trees was among the three most important variables.

Response to temperature

Examining the partial dependence of the temperature variables in our models suggest that sage-grouse avoided extreme temperatures. Partial dependence plots showed that within each season, sage-grouse were most likely to select moderate temperatures and avoided extremes. In Buckskin, the probability of sage-grouse selecting areas of the landscape dropped quickly and approached zero where temperatures in Summer exceeded roughly 35 °C, or 28 °C in Autumn (Figure 2). In Steptoe, the effect was similar but not as clear (Figure 3). Sage-grouse also selected locations with moderate minimum temperature in Summer, Autumn, and Spring in both study areas. In Winter, the probability of sage-grouse selecting habitat decreased rapidly where temperatures were below a minimum temperature of -17 °C but then plateaued (Figure 4). Similarly, maximum temperature in Steptoe was not as limiting to the landscape selected by sage-grouse as in Buckskin—the rate of change of partial dependence was slower across the available temperature range in each season and the range of temperatures where selection was most likely was less distinct.

These results indicate the importance of temperature in sage-grouse seasonal habitat selection, but do not in themselves show how the birds respond to temperature. The two-way partial dependence plots we built demonstrate the choices sage-grouse tend to make during thermal extremes. In Summer, measures of partial

dependence show that sage-grouse used areas closer to trees when maximum temperature was high, especially when it was greater than ~ 25 °C. (Figure 5). Though sage-grouse rely on sagebrush, our results indicate that they did not select large or contiguous patches of sagebrush during high summer heat in Buckskin (Figure 6). Sage-grouse likewise tended to avoid the coldest temperatures during Winter, but during these temperatures, they were more likely to be nearer to trees. In particular, when Winter minimum temperature was less than -16 °C, sage-grouse were likely to be less than 50 m from trees (Figure 7). In contrast, sage-grouse in Steptoe were more likely to avoid treed areas during extreme heat trees—when Summer maximum temperature was above 30 °C, selection was most likely > 1500 m from trees (Figure 8). Instead, at those higher temperatures Steptoe sage-grouse were likely to select areas of moderate to high sagebrush patch CAI, though that trend was weaker than selection for trees in Buckskin (Figure 9). Further, sage-grouse in Buckskin did not show strong selection for areas near trees during the highest or lowest temperatures of Autumn and Spring, when those high and low temperatures were less extreme than Summer and Winter (Figure 11).

There was also an effect of topography interacting with temperature on bird locations. In Buckskin, sage-grouse selected areas of greater topographic heterogeneity during Summer heat (Figure 12a). When maximum temperature was above 30 °C, selection was most likely at moderate to high values of heterogeneity (THI400 > 4800). The effect of topographic heterogeneity was less clear in Steptoe during Summer, where sage-grouse selected moderately rugged terrain but with less difference in selection across the ranges in maximum temperature and heterogeneity, with the highest selection rate where THI400 was 7000 – 12000 (Figure 12b). More rugged terrain exists in both study areas than is represented in the GPS location dataset, especially in Steptoe, but fell outside of the home ranges used to define “available” for this 3rd order selection process.

DISCUSSION

Temperature differences in study areas

The temperature data we recorded revealed differences in our Buckskin (Utah) and Steptoe (Nevada) study areas that were not clear using the coarser-scale PRISM data. PRISM data suggested that the two were nearly identical in average temperature and that Steptoe was drier. We did not measure precipitation, but measurements collected from temperature data loggers suggested that Buckskin was slightly warmer than Steptoe on average across the entire year. This suggests that while data like PRISM is critical for understanding many broad-scale patterns, including for sage-grouse, it is also essential to understand how temperature varies and drives ecological phenomena at biologically relevant scales. For a study of third-order habitat selection where individual home ranges may not cover more than a few pixels of PRISM data, there may be variation in temperature at finer scales that drives individuals’ choices that would be missed by coarser-scale data. For example, if simply considering PRISM data, Steptoe may have appeared to be the less suitable of the two areas, though we did not build RF models of selection using PRISM data for comparison.

Furthermore, temperatures in both study areas during the study period (June 2018 – November 2020) were higher than the period currently used to define climatic norms (1990 – 2020). The difference was small but given the differences we found in habitat selection between study areas, it may be enough to reach a threshold in thermal stress beyond which sage-grouse select habitat differently. Ongoing climate change is likely to drive shifts in sagebrush distribution and ecosystem composition (Schlaepfer et al. 2012b, Evers et al. 2013, Kleinhesselink and Adler 2018, Snyder et al. 2019), and species in Great Basin lowlands are likely to face extirpation without adequate thermal refuge (Warren et al. 2014). As that process continues, it will be increasingly important to identify potential environmental thresholds, how sensitive species like sage-grouse are likely to respond, the habitat that may provide refuge in times and places that exceed these thresholds, and how managers can plan for and mitigate negative impacts.

Response to temperature

Our results suggest that sage-grouse select habitat in response to temperature and that thermal extremes may be limiting. However, we also found that sage-grouse use land cover—and to a lesser extent, topography—as shelter from those extremes. When temperatures were highest, sage-grouse were more likely to select habitat in either more contiguous sagebrush or nearer to trees. In the warmer study area, Buckskin, sage-grouse selected habitat nearer to trees while in Steptoe they selected sagebrush cover. To our knowledge, this is the first time that any study has documented how sage-grouse habitat selection varies in response to temperature, though other research has detected wildlife responding to temperature at similarly fine scales (Varner and Dearing 2014), including Galliformes (Hovick et al. 2014, Londe et al. 2021). Where temperature at fine scales can be decoupled from larger patterns and provide suitable thermal refugia, it is critical to identify the characteristics of the landscape that foster suitable microhabitat (Rodhouse et al. 2010, Varner and Dearing 2014). Some of the clearest evidence of the influence of temperature in this study is through measures of variable importance and model performance. In each of the eight models that included temperature, all three temperature covariates were among the five most important variables. Further, including temperature consistently improved model performance compared to models without temperature covariates, especially in Buckskin in Summer. While it is clear that climate informs sage-grouse distributions and populations (Blomberg et al. 2012, Coates et al. 2016b, 2018, Acevedo 2021) and climate change is likely to negatively impact sagebrush cover in the southern Great Basin (Kleinhesselink and Adler 2018), it is important to explore potential mechanisms of individual habitat selection that drive those larger scale patterns as we have in this study.

In examining two-way partial dependence plots in combination with measures of variable importance and model performance, the impact of temperature on selection and where sage-grouse and characteristics of thermal refugia are clear. Combined, our results indicate that sage-grouse respond to temperature, but that other variables play a strong role in selection. If they did not, there would be no interaction between temperature and other variables, and at extreme temperatures there would always be low selection. On the contrary, sage-grouse are likely forced to make decisions that balance resource acquisition and the potentially competing risks of predation and thermal stress, similar to the tradeoffs faced by greater prairie chickens (*Tympanuchus cupido* [Londe et al. 2021]). For example, sage-grouse may be exposing themselves to greater risk of predation by spending time near the cool shade of trees, balanced against the risk of hyperthermia in sagebrush patches during high temperatures, which may explain some past findings of apparent high risk selection by sage-grouse (Cutting et al. 2019). Our data clearly support this, especially in Buckskin. In Spring and Autumn, when thermal extremes were less common, sage-grouse in Buckskin showed less selection for areas near trees than during the higher maximum temperature in Summer. While metrics of vegetation cover and activity such as Normalized Difference Vegetation Index (NDVI) are important for sage-grouse (Dinkins et al. 2017, Stoner et al. 2020), the grouse in this study generally selected areas with moderate temperatures and avoided extremes where possible, suggesting that temperature also drives selection. In Steptoe and Buckskin, most of the mesic habitat, which sage-grouse tend to select during late brood rearing (summer), is not treed riparian areas like in some areas of sage-grouse distribution, and there is likely little direct correlation between tree cover and mesic resources. Were sage-grouse primarily selecting based on NDVI and mesic resources, then we would not have detected sage-grouse selection for areas close to trees during higher temperatures, as those areas are not rich in mesic resources. Instead, sage-grouse would have continued to avoid trees because they could exploit the resources of mesic areas without incurring the risk of predation near trees. Furthermore, the fact that sage-grouse in our two study areas did not select for the same land cover in response to thermal extremes suggests that vegetation activity (e.g., NDVI) is not their only limitation, and there is cryptic fragmentation of suitable sagebrush habitat in Buckskin, while in Steptoe the contiguous sagebrush provides enough thermal cover that sage-grouse there are not forced to shelter near trees.

Similarly, several previous studies have found negative effects of terrain ruggedness on sage-grouse (Doherty et al. 2008, 2010b, Knick et al. 2013, Dinkins et al. 2017). Those have largely examined larger-scale processes such as population size or lek persistence and captured a broader spatial sample of the “available” landscape.

On the other hand, other studies focused on individual habitat selection have found that in some conditions, sage-grouse select more rugged terrain than expected, especially in marginal habitat (Dinkins et al. 2014, Beers and Frey 2022a). Like those, this study found that sage-grouse in some cases select more rugged terrain than expected. This may be in part because some of the more heterogeneous topography in these study areas tended to be near valley edges, where sage-grouse appeared to use taller and denser land cover (trees and dense sagebrush) for thermal refuge. However, the fact that measures of topographic heterogeneity were often among the most important variables in the RF models shows that the terrain itself also featured in sage-grouse selection. It may be that moderately rugged terrain fosters snow deposition, accumulation, and retention in winter and spring (Winstral et al. 2002, Jost et al. 2007). In cold extremes, sage-grouse could use that snow as thermal cover. That retained snow may then allow the persistence of more mesic microhabitat during summer. Our study was focused at smaller scales and did not sample from a large enough area to include the mountainous terrain surrounding the study areas that might have been defined as available habitat in a 2nd or 1st order selection process, which may have allowed me to detect the effects of topography on habitat selection at fine scales.

It is important to note that in our models we did not use known temperature data at the exact location of each sage-grouse GPS detection. We also did not estimate temperature at each of those points based on interpolating temperature between the nearest data loggers. Instead, we used modeled outputs that represent detected trends of temperature within each study area and season, hypothesizing that sage-grouse selection trends will correspond to those of temperature. This may mean that these temperature data lack precision in their interpolation and there would be a benefit to implementing a temperature interpolation method that allows us to model the impacts on individual sage-grouse movements. In the case of both summer heat and winter cold, when sage-grouse make selections to avoid thermal stress, they are likely to experience even more extreme temperatures than we detected. We intentionally positioned data loggers to avoid direct sun exposure and removed data points where the logger nonetheless received direct sunlight. Yet, sage-grouse experience heating from direct sunlight and must make decisions to avoid it if stressed, seeking shade from land cover or otherwise moving to a cooler area, such as by changing elevation or habitat type. Similarly, in both sites there were some data loggers that appeared to have been covered in snow for periods of the winter given their small diel range in light intensity detected compared to that of other loggers. Because the data loggers were therefore insulated, these data likely do not capture all of the coldest events, and modeled Winter minimum temperature may be higher than what occurred. However, the loggers also likely reflect the temperatures that sage-grouse experience, as they are known to burrow into snow for shelter during extreme winter events (Beck 1977, Back et al. 1987).

Conservation implications

Our findings may point toward a mechanism limiting the extent of the sage-grouse distribution on their warm range margin—inadequate refuge from thermal stress and a cryptic fragmentation that inadequacy creates. In both Buckskin and Steptoe, there are large areas of contiguous sagebrush. In Buckskin, those areas are mostly at lower elevations within Buckskin Valley and the cooler, high elevation available habitat is dominated by trees: pinyon pine, juniper, Gambel oak, mountain mahogany, and some aspen. In Steptoe, there are much larger patches of contiguous sagebrush in both the valley bottom and in a few patches at mid to upper elevations that have more area far from dense tree cover. While Steptoe grouse avoided tree cover during high summer temperatures, generally selecting habitat more than 1800 m from trees, in Buckskin there is little area that is more than 800 m from tree cover. Therefore, Steptoe sage-grouse have more habitat in which to escape from thermal stress without incurring greater predation risk, while in the Buckskin site they more often choose to shelter in riskier habitat. While sage-grouse in some areas of Steptoe likely also face that tradeoff, that valley is much larger and there is more area where sage-grouse do not have to choose between thermal stress and predation risk. Buckskin may therefore act as a portent for what may occur in Steptoe given continued warming, sagebrush loss, and conifer encroachment.

Sage-grouse have been observed using trees in the past or using areas with tree cover great enough to reduce survival (Baruch-Mordo et al. 2013, Coates et al. 2017, Beers and Frey 2022a), but the reason for that risky

choice has been unclear. A potential explanation suggested by our results is that in areas where temperature is limiting, especially in summer heat and fragmented habitat, sage-grouse may be impelled to incur the risk of predation to avoid thermal stress.

In contrast with the long-term climate data from PRISM, our data indicated that Utah’s Buckskin Valley is marginally warmer than Nevada’s Steptoe Valley. In combination with the fact that our results suggest that sage-grouse respond to extreme operative temperatures in habitat selection, this underscores the fact that temperature varies at multiple scales, and that it is potentially hazardous to infer fine-scale processes in either temperature or wildlife response to it based on larger patterns (Gillingham et al. 2012, Gollan et al. 2015). Instead, studies should evaluate potential predictor variables at more biologically relevant scales. Though preference at fine scales for moderate temperatures has been demonstrated for other potentially threatened species and environments (Scherrer and Korner 2011, Varner and Dearing 2014), including for greater prairie chicken (Hovick et al. 2014, Londe et al. 2021), it has not been demonstrated for greater sage-grouse. Sage-grouse in the southern great basin are likely to face a future with a more xeric environment and declining sagebrush cover (Tredennick et al. 2016, Kleinhesselink and Adler 2018). Because sagebrush is sensitive to climate (Schlaepfer et al. 2014, Tredennick et al. 2016, Renwick et al. 2018), as a sagebrush obligate, sage-grouse will be negatively impacted by its range retracting along the southern range margin. Their range limit, therefore, may be defined by a combination of sagebrush cover, exposure to extreme heat, and the extent of trees.

As the climate continues to change, it will be important to identify or even foster potential microrefugia for sage-grouse. Hotter summers and less sagebrush cover will likely make their current southern range margin even less tenable through thermal stress and loss of forage. Compounded by increased threat of avian predation due to ongoing pinyon-juniper encroachment and potential ecological traps (Coates et al. 2017, Pratt and Beck 2021), sage-grouse will face greater threats in the future where thermal stress drives them to make risky habitat selection. Even on their fragmented southern range margin, there may be some suitable microrefugia or holdouts as climate changes if there are large enough areas of contiguous sagebrush and some decoupling from regional climate at local scales (Dobrowski 2011, Hannah et al. 2014). Yet that is only if the limiting climatic factors for sage-grouse decouple from regional trends in the landscapes they occupy and if ecosystem managers take steps to foster suitable microhabitats (Hylander et al. 2015, Selwood et al. 2019). That may mean adopting a comprehensive, pragmatic approach to identify potential microrefugia (Ashcroft et al. 2012), evaluate ecosystem resistance and resilience (Chambers et al. 2007, Ricca et al. 2018), and assess local to regional scale factors to determine what actions are appropriate in different areas of sage-grouse habitat (Doherty et al. 2016, Lynch et al. 2021). For sage-grouse, that may mean creating some areas of mesic resources to offer thermal refuge during extreme heat (Donnelly et al. 2018). Ironically, it may also entail leaving some tree cover where sage-grouse will be exposed to thermal stress and do not have other adequate cover. Conifer removal efforts should prioritize areas where sage-grouse are likely to experience thermal stress and do not have shelter from avian predators. In particular, sage-grouse would likely be most vulnerable during thermal extremes in flatter, more open terrain with less intact sagebrush patches where they are less able to hide from avian predators (Dinkins et al. 2017). For that purpose, lone trees would likely remain dangerous and provide little shelter, but small clusters of dense trees could be useful.

Conclusion

In this study we identified when temperature impact sage-grouse habitat selection and described their response to mitigate thermal stress. Though this has been a focus of study for other species of conservation concern, this is the first study to address temperature effects on sage-grouse habitat selection at a fine scale. We found that extreme temperatures may be limiting, but that sage-grouse response to those temperatures likely depend on what refuge habitat is available. In the larger study area with greater extents of contiguous sagebrush, marginally cooler temperatures, and more patches of sagebrush at higher elevations, sage-grouse tended to select those patches during high summer temperatures. In the smaller study area with less apparent refuge, sage-grouse used areas close to trees when temperatures were most extreme. Selection depends on the local environment and always involves tradeoffs—in this case it appears there may be some threshold

in the combination of thermal exposure and sagebrush availability beyond which sage-grouse are more likely to risk exposure to avian predators. This suggests thermal stress contributing to cryptic fragmentation as a mechanism limiting greater sage-grouse in areas of their southern range margin and shows that ecosystem management in the Great Basin must account for regional and local factors of climate and sagebrush loss and fragmentation to protect the sagebrush and its imperiled species into the future.

LITERATURE CITED

- Acevedo, C. R. 2021. Spatio-temporal Population Dynamics of Nevada Greater Sage-grouse from 2000-2018. University of Nevada, Reno.
- Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983–994.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43:1223–1232.
- Arntzen, J. W., and G. Espregueira Themudo. 2008. Environmental parameters that determine species geographical range limits as a matter of time and space. *Journal of Biogeography* 35:1177–1186.
- Ashcroft, M. B., and J. R. Gollan. 2012. Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region. *International Journal of Climatology* 32:2134–2148.
- Ashcroft, M. B., J. R. Gollan, D. I. Warton, and D. Ramp. 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology* 18:1866–1879.
- Back, G. N., M. R. Barrington, and J. K. McAdoo. 1987. Sage Grouse Use of Snow Burrows in Northeastern Nevada. *The Wilson Bulletin* 99:488–490.
- Balzotti, C. S., S. G. Kitchen, and C. McCarthy. 2016. Beyond the single species climate envelope: a multifaceted approach to mapping climate change vulnerability. *Ecosphere* 7.
- Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. *Biological Conservation* 167:233–241.
- Beck, T. D. I. 1977. Sage Grouse Flock Characteristics and Habitat Selection in Winter. *The Journal of Wildlife Management* 41:18–26.
- Beers, A. T., and S. N. Frey. 2022. Greater sage-grouse habitat selection varies across the marginal habitat of its lagging range. *Ecosphere* 13:e4146.
- Beever, E. A., L. E. Hall, J. Varner, A. E. Loosen, J. B. Dunham, M. K. Gahl, F. A. Smith, and J. J. Lawler. 2017. Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment* 15:299–308.
- Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B. P. Kotler, and D. Saltz. 2011. Integrating animal behavior and conservation biology: A conceptual framework. *Behavioral Ecology* 22:236–239.
- Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. *Ecosphere* 3:art55.
- Braun, C. E. 1998. Sage grouse declines in western North America: What are the problems? *Proceedings of the Western Association of State Fish and Wildlife Agencies* 78:139–156.
- Breiman, L. 2001. Random Forests. *Machine Learning* 45:5–32.

Calenge, C. 2017. adehabitatHR.

Calle, M. L., and V. Urrea. 2011. Letter to the editor: Stability of Random Forest importance measures. *Briefings in Bioinformatics* 12:86–89.

Chambers, J., R. Mountain, U. F. Service, S. Campbell, U. Natural, R. Conservation, J. Maestas, U. Natural, R. Conservation, J. Cartwright, and G. Survey. 2007. Chapter 24 : Sagebrush ecosystem resilience and resistance:196–206.

Chen, C., A. Liaw, and L. Breiman. 2004. Using Random Forest to Learn Imbalanced Data. Page University of California Tech Reports. Berkeley, CA.

Chen, I.-C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333:1024–1026.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. Ben Gustafson, P. Ziegler, and M. L. Casazza. 2017. Pinyon and Juniper Encroachment into Sagebrush Ecosystems Impacts Distribution and Survival of Greater Sage-Grouse. *Rangeland Ecology and Management* 70:25–38.

Coates, P. S., B. G. Prochazka, M. A. Ricca, B. J. Halstead, M. L. Casazza, E. J. Blomberg, B. E. Brussee, L. Wiechman, J. Tebbenkamp, S. C. Gardner, and K. P. Reese. 2018. The relative importance of intrinsic and extrinsic drivers to population growth vary among local populations of Greater Sage-Grouse: An integrated population modeling approach. *The Auk* 135:240–261.

Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, J. Blomberg, C. A. Hagen, M. L. Casazza, P. S. Coates, M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, and T. Kroger. 2016. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 113:12745–12750.

Cohen, J. 1960. A Coefficient of Agreement for Nominal Scales. *Educational and Psychological Measurement* XX:37–46.

Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229–234.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats Conservation Assessment and Sagebrush Habitats. Unpublished report.

Cushman, S. A., K. Gutzweiler, J. S. Evans, and K. Mcgarigal. 2010. The Gradient Paradigm: A Conceptual and Analytical Framework for Landscape Ecology. Pages 83–108 *in* S. A. Cushman and F. Huettmann, editors. *Spatial Complexity, Informatics, and Wildlife Conservation*. Springer.

Cushman, S. A., and T. N. Wasserman. 2018. Landscape Applications of Machine Learning: Comparing Random Forests and Logistic Regression in Multi-Scale Optimized Predictive Modeling of American Marten Occurrence in Northern Idaho, USA. Pages 185–203 *in* G. Humphries, D. Magness, and F. Huettmann, editors. *Machine Learning for Ecology and Sustainable Natural Resource Management*. Springer.

Cutting, K. A., J. J. Rotella, S. R. Schro, M. R. Frisina, J. A. Waxe, E. Nunlist, and B. F. Sowell. 2019. Maladaptive nest-site selection by a sagebrush dependent species in a grazing-modified landscape. *Journal of Environmental Management* 236:622–630.

Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584.

De’ath, G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88:243–251.

- Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014. Greater Sage-Grouse (*Centrocercus urophasianus*) hen survival: Effects of raptors, anthropogenic and landscape features, and hen behavior. *Canadian Journal of Zoology* 92:319–330.
- Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, S. N. Frey, J. B. Dinkins, M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2017. Greater Sage-Grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. *The Condor: Ornithological Applications* 116:629–642.
- Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* 17:1022–1035.
- Doherty, K. E., J. S. Evans, P. S. Coates, L. M. Juliusson, and B. C. Fedy. 2016. Importance of regional variation in conservation planning: a rangewide example of the Greater Sage-Grouse. *Ecosphere* 7:1–27.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater Sage-Grouse Nesting Habitat: The Importance of Managing at Multiple Scales. *Journal of Wildlife Management* 74:1544–1553.
- Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater Sage-Grouse Winter Habitat Selection and Energy Development. *Journal of Wildlife Management* 72:187–195.
- Donnelly, J. P., J. D. Tack, B. W. Allred, D. Perret, N. L. Silverman, V. J. Dreitz, J. D. Maestas, and D. E. Naugle. 2018. Seasonal drought in North America’s sagebrush biome structures dynamic mesic resources for sage-grouse. *Ecology and Evolution* 8:12492–12505.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802–813.
- Emm, G., B. Lister, J. Barbee, and B. Crowell. 2019. 2019 Nevada Greater Sage-grouse Conservation Plan Sagebrush Ecosystem Program. Carson City, Nevada.
- Evers, L. B., R. F. Miller, P. S. Doescher, M. Hemstrom, P. Ronald, L. B. Evers, R. F. Miller, P. S. Doescher, M. Hemstrom, and R. P. Neilson. 2013. Simulating Current Successional Trajectories in Sagebrush Ecosystems With Multiple Disturbances Using a State-and-Transition Modeling Framework. *Rangeland Ecology & Management* 66:313–329.
- Fieberg, J. R., J. D. Forester, G. M. Street, D. H. Johnson, A. A. Archmiller, and J. Matthiopoulos. 2018. Used-habitat calibration plots: a new procedure for validating species distribution, resource selection, and step-selection models. *Ecography* 41:737–752.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation* 24:38–49.
- Frey, S. N., R. Curtis, and K. Heaton. 2013. Response of a small population of greater sage-grouse to tree removal: Implications of limiting factors. *Human-Wildlife Interactions* 7:260–272.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for Trapping Sage Grouse in Colorado. *Wildlife Society Bulletin* 10:224–231.
- Gillingham, P. K., B. Huntley, W. E. Kunin, and C. D. Thomas. 2012. The effect of spatial resolution on projected responses to climate warming. *Diversity and Distributions* 18:990–1000.
- Gollan, J. R., D. Ramp, and M. B. Ashcroft. 2015. Contrasting topoclimate, long-term macroclimatic averages, and habitat variables for modelling ant biodiversity at landscape scales. *Insect Conservation and Diversity* 8:43–53.
- Greenwell, B. M. 2017. pdp: An R Package for Constructing Partial Dependence Plots.
- Group, P. C. 2020. PRISM Gridded Climate Data. Oregon State University.

- Hampe, A., and R. J. Petit. 2005. Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters* 8:461–467.
- Hannah, L., L. Flint, A. D. Syphard, M. a. Moritz, L. B. Buckley, and I. M. McCullough. 2014. Fine-grain modeling of species’ response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution* 29:390–397.
- Hanser, S. E., and S. T. Knick. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pages 475–488 *Greater Sage-Grouse: Ecology and Conservation of a Landscape Species and Its Habitats*. Reston, VA.
- Hesselbarth, M. H. K., M. Sciaini, J. Nowosad, S. Hanss, L. J. Graham, J. Hollister, K. A. With, F. Prive, J. VanDerWal, and M. Strimas-Mackey. 2019. *landscapemetrics: Landscape Metrics for Categorical Map Patterns*.
- Hollister, J., T. Shah, A. L. Robitaille, M. W. Beck, and M. Johnson. 2017. *elevatr: Access Elevation Data from Various APIs*. CRAN.
- Hovick, T. J., R. D. Elmore, B. Wallred, S. D. Fuhlendorf, and D. K. Dahlgren. 2014. Landscapes as a moderator of thermal extremes: A case study from an imperiled grouse. *Ecosphere* 5:1–12.
- Hylander, K., J. Ehrlen, M. Luoto, and E. Meineri. 2015. Microrefugia: Not for everyone. *Ambio* 44:60–68.
- Jenness, J., B. Brost, and P. Beier. 2013. *Land Facet Corridor Designer: Extension for ArcGIS*. Jenness Enterprises.
- Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* 61:65–71.
- Jost, G., M. Weiler, D. R. Gluns, and Y. Alila. 2007. The influence of forest and topography on snow accumulation and melt at the watershed-scale. *Journal of Hydrology* 347:101–115.
- Keith, D. A., H. R. Akcakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araujo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4:560–563.
- Kirol, C. P., J. L. Beck, S. V. Uzurbazar, M. J. Holloran, and S. N. Miller. 2015. Identifying Greater Sage-Grouse source and sink habitats for conservation planning in an energy development landscape. *Ecological Applications* 25:968–990.
- Kleinhesselink, A. R., and P. B. Adler. 2018. The response of big sagebrush (*Artemisia tridentata*) to interannual climate variation changes across its range. *Ecology* 99:1139–1149.
- Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: Implications for population connectivity across their western range, U.S.A. *Ecology and Evolution* 3:1539–1551.
- Kuhn, M. 2016. Package “caret.”
- Landis, J. R., and G. G. Koch. 1977. The Measurement of Observer Agreement for Categorical Data. *Biometrics* 33:159–174.
- Lawson, C. R., J. A. Hodgson, R. J. Wilson, and S. A. Richards. 2014. Prevalence, thresholds and the performance of presence-absence models. *Methods in Ecology and Evolution* 5:54–64.
- Lima, F. P., F. Gomes, R. U. I. Seabra, D. S. Wethey, and I. Maria. 2016. Loss of thermal refugia near equatorial range limits. *Global Change Biology* 22:254–263.
- Londe, D. W., R. D. Elmore, C. A. Davis, S. D. Fuhlendorf, and T. J. Hovick. 2021. Fine-scale habitat selection limits trade-offs between foraging and temperature in a grassland bird. *Behavioral Ecology*:1–13.

- Lynch, A. J., L. M. Thompson, E. A. Beever, D. N. Cole, A. C. Engman, C. Hawkins Hoffman, S. T. Jackson, T. J. Krabbenhoft, D. J. Lawrence, D. Limpinsel, R. T. Magill, T. A. Melvin, J. M. Morton, R. A. Newman, J. O. Peterson, M. T. Porath, F. J. Rahel, G. W. Schuurman, S. A. Sethi, and J. L. Wilkening. 2021. Managing for RADical Ecosystem Change: Applying the Resist, Accept, or Direct (RAD) Framework. *Frontiers in Ecology and the Environment* 19:461–469.
- MacKenzie, D. I. 2005. What are the Issues with Presence-Absence Data for Wildlife Managers? *Journal of Wildlife Management* 69:849–860.
- McDonald, L., B. Manly, F. Huettmann, and W. Thogmartin. 2013. Location-only and use-availability data: analysis methods converge. *Journal of Animal Ecology* 82:1120–1124.
- Mi, C., F. Huettmann, Y. Guo, X. Han, and L. Wen. 2017. Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence. *PeerJ* 5:e2849.
- Oldfather, M. F., M. M. Kling, S. N. Sheth, N. C. Emery, and D. D. Ackerly. 2020. Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. *Global Change Biology* 26:1055–1067.
- Olsen, A. C., J. P. Severson, J. D. Maestas, D. E. Naugle, J. T. Smith, J. D. Tack, K. H. Yates, and C. A. Hagen. 2021. Reversing tree expansion in sagebrush steppe yields population-level benefit for imperiled grouse. *Ecosphere* 12.
- Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285–297.
- Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual of Ecology, Evolution and Systematics* 37:637–669.
- Patten, M. A., D. H. Wolfe, E. Syochat, and S. K. Sherrod. 2007. Effects of Microhabitat and Microclimate Selection on Adult Survivorship of the Lesser Prairie-Chicken. *The Journal of Wildlife Management* 69:1270–1278.
- Pecl, G. T., M. B. Araujo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengard, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, and M. Tuanmu. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being 9214.
- Picardi, S., T. Messmer, B. Crabb, M. Kohl, D. Dahlgren, N. Frey, R. Larsen, and R. Baxter. 2020. Predicting greater sage-grouse habitat selection at the southern periphery of their range. *Ecology and Evolution* 10:13451–13463.
- Pratt, A. C., and J. L. Beck. 2021. Do greater sage-grouse exhibit maladaptive habitat selection? *Ecosphere* 12.
- Pratt, A. C., K. T. Smith, and J. L. Beck. 2017. Environmental cues used by Greater Sage-Grouse to initiate altitudinal migration. *The Auk* 134:628–643.
- Prochazka, B. G., P. S. Coates, M. A. Ricca, M. L. Casazza, K. B. Gustafson, and J. M. Hull. 2017. Encounters with Pinyon-Juniper Influence Riskier Movements in Greater Sage-Grouse Across the Great Basin. *Rangeland Ecology and Management* 70:39–49.
- Rather, T. A., S. Kumar, and J. A. Khan. 2020. Multi-scale habitat selection and impacts of climate change on the distribution of four sympatric meso-carnivores using random forest algorithm. *Ecological Processes* 9.

- Reisinger, R. R., A. S. Friedlaender, A. N. Zerbini, D. M. Palacios, V. Andrews-goff, L. D. Rosa, M. Double, K. Findlay, and C. Garrigue. 2021. Combining Regional Habitat Selection Models for Large-Scale Prediction: Circumpolar Habitat Selection of Southern Ocean Humpback Whales. *Remote Sensing* 13.
- Renwick, K. M., C. Curtis, A. R. Kleinhesselink, D. Schlaepfer, B. A. Bradley, C. L. Aldridge, B. Poulter, and P. B. Adler. 2018. Multi-model comparison highlights consistency in predicted effect of warming on a semi-arid shrub. *Global Change Biology* 24:424–438.
- Ricca, M. A., and P. S. Coates. 2020. Integrating Ecosystem Resilience and Resistance Into Decision Support Tools for Multi-Scale Population Management of a Sagebrush Indicator Species. *Frontiers in Ecology and the Environment* 7:1–22.
- Ricca, M. A., P. S. Coates, K. B. Gustafson, B. E. Brussee, J. C. Chambers, S. P. Espinosa, S. C. Gardner, S. Lisius, P. Ziegler, D. J. Delehanty, and M. L. Casazza. 2018. A conservation planning tool for Greater Sage-grouse using indices of species distribution, resilience, and resistance. *Ecological Applications* 28:878–896.
- Robinson, R. L. M., A. Palczewska, J. Palczewski, and N. Kidley. 2017. Comparison of the Predictive Performance and Interpretability of Random Forest and Linear Models on Benchmark Data Sets. *Journal of Chemical Information and Modeling* 57:1773–1792.
- Rodhouse, T. J., E. a. Beaver, L. K. Garrett, K. M. Irvine, M. R. Jeffress, M. Munts, and C. Ray. 2010. Distribution of American pikas in a low-elevation lava landscape: conservation implications from the range periphery. *Journal of Mammalogy* 91:1287–1299.
- Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18:235–249.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323–335.
- Rull, V. 2009. Microrefugia. *Journal of Biogeography* 36:481–484.
- Runge, C. A., J. C. Withey, D. E. Naugle, J. E. Fargione, K. J. Helmstedt, A. E. Larsen, S. Martinuzzi, and J. D. Tack. 2019. Single species conservation as an umbrella for management of landscape threats. *Plos One*:1–17.
- Scherrer, D., and C. Korner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38:406–416.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012a. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. *Ecography* 35:374–384.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012b. Consequences of declining snow accumulation for water balance of mid-latitude dry regions. *Global Change Biology* 18:1988–1997.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2014. Synthesis Natural Regeneration Processes in Big Sagebrush (*Artemisia tridentata*). *Rangeland Ecology & Management* 67:344–357.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Garnder, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. Mccarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *The Condor* 106:363–376.
- Seabrook, L., C. Mcalpine, J. Rhodes, G. Baxter, A. Bradley, and D. Lunney. 2014. Determining range edges: habitat quality, climate or climate extremes? *Diversity and Distributions* 20:95–106.

- Selwood, K. E., S. C. Cunningham, and R. Mac. 2019. Beyond refuges : Identifying temporally dynamic havens to support ecological resistance and resilience to climatic disturbances. *Biological Conservation* 233:131–138.
- Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017a. Effects of Conifer Expansion on Greater Sage-Grouse Nesting Habitat Selection. *The Journal of Wildlife Management* 81:86–95.
- Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017b. Short-Term Response of Sage-Grouse Nesting to Conifer Removal in the Northern Great Basin. *Rangeland Ecology and Management* 70:50–58.
- Shoemaker, K. T., L. J. Heffelfinger, N. J. Jackson, M. E. Blum, T. Wasley, and K. M. Stewart. 2018. A machine-learning approach for extending classical wildlife resource selection analyses. *Ecology and Evolution* 8:3556–3569.
- Snyder, K. A., L. Evers, J. C. Chambers, J. Dunham, J. B. Bradford, and M. E. Loik. 2019. Effects of Changing Climate on the Hydrological Cycle in Cold Desert Ecosystems of the Great Basin and Columbia Plateau. *Rangeland Ecology & Management* 72:1–12.
- Stephanie, M., W. H. Ceri, and O. S.J. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921–931.
- Stoner, D. C., T. A. Messmer, R. T. Larsen, S. Nicki, M. T. Kohl, E. T. Thacker, and D. K. Dahlgren. 2020. Using satellite-derived estimates of plant phenological rhythms to predict sage-grouse nesting chronology. *Ecology and Evolution*:1–14.
- Street, G. M., J. R. Potts, L. Borger, J. C. Beasley, S. Demarais, J. M. Fryxell, P. D. McLoughlin, K. L. Monteith, C. M. Prokopenko, M. C. Ribeiro, A. R. Rodgers, B. K. Strickland, F. M. van Beest, D. A. Bernasconi, L. T. Beumer, G. Dharmarajan, S. P. Dwinell, D. A. Keiter, A. Keuroghlian, L. J. Newediuk, J. E. F. Oshima, O. Rhodes, P. E. Schlichting, N. M. Schmidt, and E. Vander Wal. 2021. Solving the Sample Size Problem for Resource Selection Functions. *Methods in Ecology and Evolution* 12:1–11.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–8.
- Travis, J. M. J., and C. Dytham. 2004. A method for simulating patterns of habitat availability at static and dynamic range margins. *Oikos* 104:410–416.
- Tredennick, A. T., M. B. Hooten, C. L. Aldridge, C. G. Homer, A. R. Kleinhesselink, and P. B. Adler. 2016. Forecasting climate change impacts on plant populations over large spatial extents. *Ecosphere* 7:1–16.
- Utah Public Lands Policy Coordination Office. 2019. Utah Conservation Plan For Greater Sage-Grouse. Salt Lake City, USA.
- Valavi, R., J. Elith, J. J. Lahoz-Monfort, and G. Guillera-Arroita. 2021. Modelling species presence-only data with random forests. *Ecography* 44:1731–1742.
- Vale, C. G., P. Tarroso, and J. C. Brito. 2014. Predicting species distribution at range margins: Testing the effects of study area extent, resolution and threshold selection in the Sahara-Sahel transition zone. *Diversity and Distributions* 20:20–33.
- Varner, J., and M. D. Dearing. 2014. The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments. *PLoS ONE* 9:e104648.
- Varner, J., J. J. Horns, M. S. Lambert, E. Westberg, J. S. Ruff, K. Wolfenberger, E. A. Beever, and M. D. Dearing. 2016. Plastic pikas: Behavioural flexibility in low-elevation pikas (*Ochotona princeps*). *Behavioural*

Warren, D. R., J. B. Dunham, and D. Hockman-Wert. 2014. Geographic Variability in Elevation and Topographic Constraints on the Distribution of Native and Nonnative Trout in the Great Basin. *Transactions of the American Fisheries Society* 143:205–218.

Winstral, A., K. Elder, and R. E. Davis. 2002. Spatial Snow Modeling of Wind-Redistributed Snow Using Terrain-Based Parameters. *Journal of Hydrometeorology* 3:524–538.

Wright, M. N., S. Wager, and P. Probst. 2021. ranger: A Fast Implementation of Random Forests. R Forge.

Yu, H., A. R. Cooper, and D. M. Infante. 2020. Improving species distribution model predictive accuracy using species abundance: Application with boosted regression trees. *Ecological Modelling* 432.

Zhang, L., F. Huettmann, S. Liu, P. Sun, Z. Yu, and X. Zhang. 2019. Classification and regression with random forests as a standard method for presence-only data SDMs: A future conservation example using China tree species. *Ecological Informatics* 52:46–56.

FIGURES AND TABLES

Table 1. Mean temperatures (degC) in each study area and season and the p-value for a t-test evaluating the differences in temperatures between study areas.

Season	Steptoe mean	Buckskin mean	p-value
All	1.85	3.50	<0.0001
Autumn	1.83	3.48	<0.0001
Winter	-11.32	-10.02	<0.0001
Spring	-2.39	-1.77	<0.0001
Summer	13.92	15.81	<0.0001

Table 2. Model performance for each Study Area – Season combination, including and excluding temperature covariates, measured by true skill statistic (TSS), Cohen’s kappa, sensitivity, correlation in used-habitat calibration (UHC), and the mean of those metrics. Mean performance difference shows the mean difference in model performance for a Study Area – Season model when including temperature covariates compared to excluding them.

Study Area	Season	Temperature covariates	TSS	Kappa	Sensitivity	UHC correlation	Mean Performance
Steptoe	Autumn	Yes	0.6988	0.6825	0.8544	0.9516	0.7968
Steptoe	Autumn	No	0.5792	0.5492	0.8190	0.9853	0.7332
Steptoe	Winter	Yes	0.7125	0.7024	0.7854	0.9423	0.7857
Steptoe	Winter	No	0.6271	0.6049	0.7387	0.9648	0.7339
Steptoe	Spring	Yes	0.6389	0.6289	0.8594	0.9606	0.7720
Steptoe	Spring	No	0.5640	0.5312	0.8248	0.9523	0.7181
Steptoe	Summer	Yes	0.7017	0.7298	0.8429	0.9501	0.8061
Steptoe	Summer	No	0.6221	0.6321	0.7861	0.9446	0.7462
Buckskin	Autumn	Yes	0.7053	0.7284	0.9012	0.9659	0.8252
Buckskin	Autumn	No	0.6937	0.8089	0.7820	0.9590	0.8109
Buckskin	Winter	Yes	0.7269	0.8080	0.8213	0.9559	0.8280
Buckskin	Winter	No	0.7239	0.7822	0.8579	0.9327	0.8242
Buckskin	Spring	Yes	0.8358	0.6759	0.9318	0.9154	0.8397
Buckskin	Spring	No	0.8160	0.7109	0.8349	0.8970	0.8147
Buckskin	Summer	Yes	0.9224	0.9123	0.9550	0.9713	0.9403

Study Area	Season	Temperature covariates	TSS	Kappa	Sensitivity	UHC correlation	Mean Performance
Buckskin	Summer	No	0.8269	0.8349	0.8215	0.9401	0.8559

Table Top five most important variables for each Study Area – Season combination model with and without temperature covariates, measured by the mean decrease in Gini index (node impurity). The possible variables included temperature minimum, maximum, and difference (T_{\min} , T_{\max} , T_{diff}); topographic position index (TPI) and topographic heterogeneity index (THI) at scales of 50 m, 200 m, and 400 m; sagebrush patch core area index (CAI) and contiguity (CONTIG); distance to tree cover (TREEDIST); and density of tree cover (TREEDEN) within 400 m and 800 m.

Study Area	Season	Temperature covariates	Top five important variables
Step toe	Autumn	Yes	T_{\min} , T_{\max} , T_{diff} , TREEDIST, CONTIG
Step toe	Winter	Yes	T_{\min} , T_{diff} , TREEDEN800, T_{\max} , THI400
Step toe	Spring	Yes	T_{\max} , T_{diff} , TREEDIST, T_{\min} , THI400, THI200
Step toe	Summer	Yes	T_{\min} , T_{diff} , TREEDIST, CONTIG, THI400
Step toe	Autumn	No	TREEDIST, THI400, THI200, TREEDEN800, CONTIG
Step toe	Winter	No	TREEDEN800, THI400, TREEDEN400, TREEDIST, THI200
Step toe	Spring	No	TREEDIST, THI400, THI200, TPI400, TREEDEN800
Step toe	Summer	No	TREEDIST, THI400, CONTIG, TREEDEN800, THI200
Buckskin	Autumn	Yes	CONTIG, TREEDEN800, T_{\min} , TREEDEN400, TREEDIST
Buckskin	Winter	Yes	T_{\min} , T_{diff} , TREEDEN800, T_{\max} , THI400
Buckskin	Spring	Yes	CONTIG, TREEDEN800, TREEDIST, T_{\min} , T_{diff}
Buckskin	Summer	Yes	T_{\min} , T_{\max} , T_{diff} , TREEDIST, CONTIG
Buckskin	Autumn	No	CONTIG, TREEDEN800, TREEDEN400, TREEDIST, THI400
Buckskin	Winter	No	TREEDEN800, CONTIG, TREEDEN400, TREEDIST, THI400
Buckskin	Spring	No	CONTIG, TREEDEN800, TREEDIST, TREEDEN400, THI400
Buckskin	Summer	No	CONTIG, TREEDEN400, TREEDEN400, TREEDIST, THI400

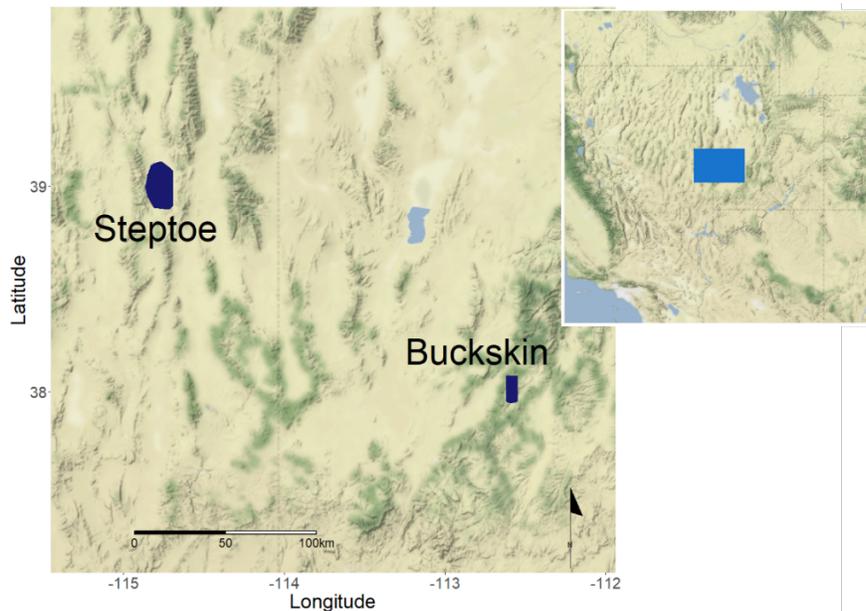


Figure 1. Study area locations in the western United States—Steptoe Valley, Nevada and Buckskin Valley, Utah—marked in dark blue with a minimum convex polygon around sage-grouse GPS data points collected there June 2019 – November 2020.

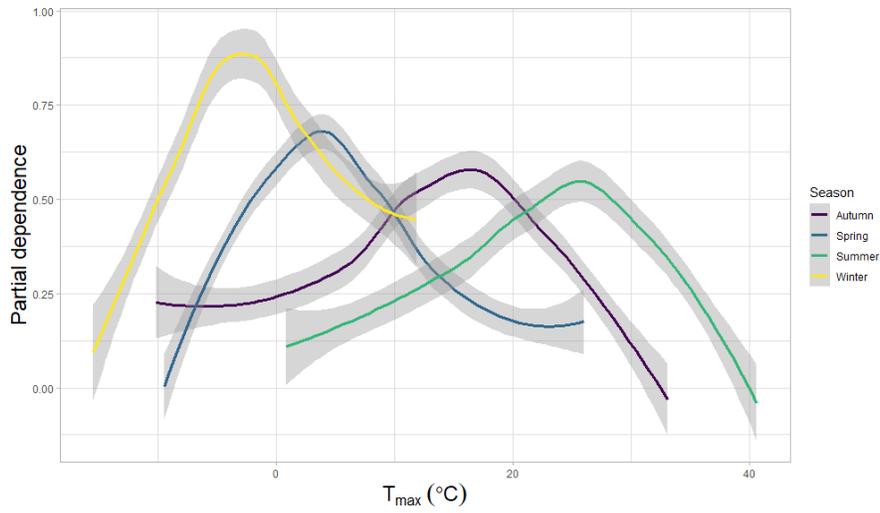


Figure 2. Marginal effect of average daily maximum temperature on sage-grouse habitat selection in Buckskin Valley, Utah across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

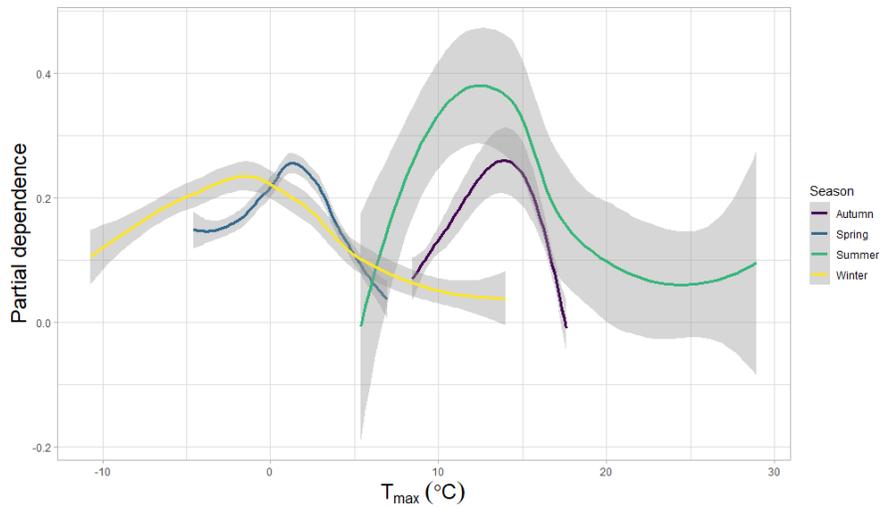
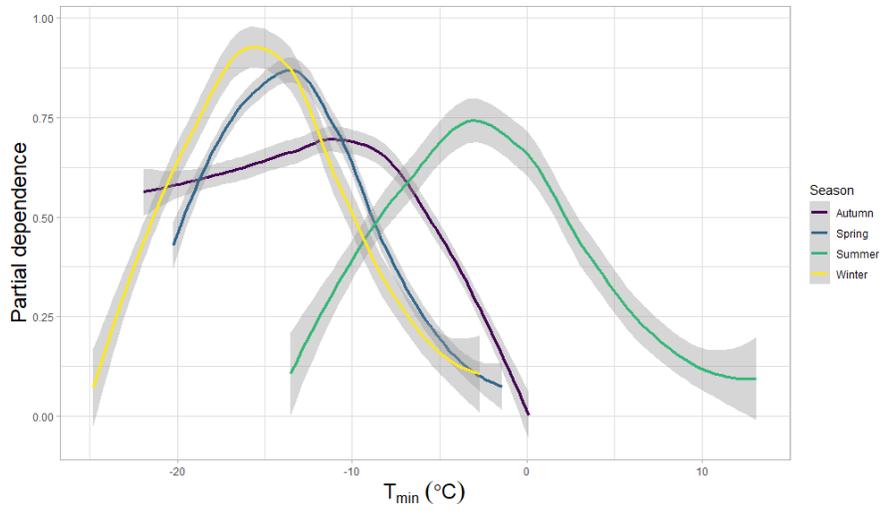


Figure 3. Marginal effect of average daily maximum temperature on sage-grouse habitat selection in Steptoe Valley, Nevada across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

a)



b)

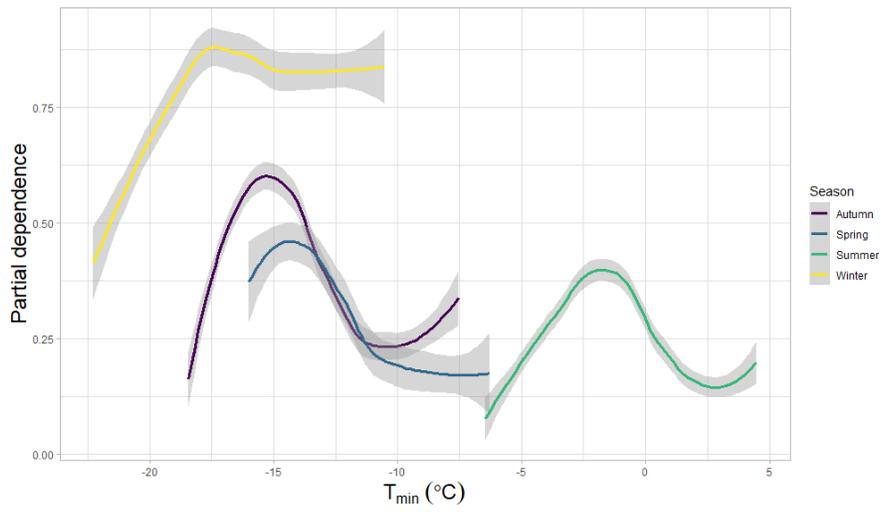


Figure 4. Marginal effect of average daily minimum temperature on sage-grouse habitat selection in **a)** Buckskin Valley, Utah and **b)** Steptoe Valley, Nevada across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

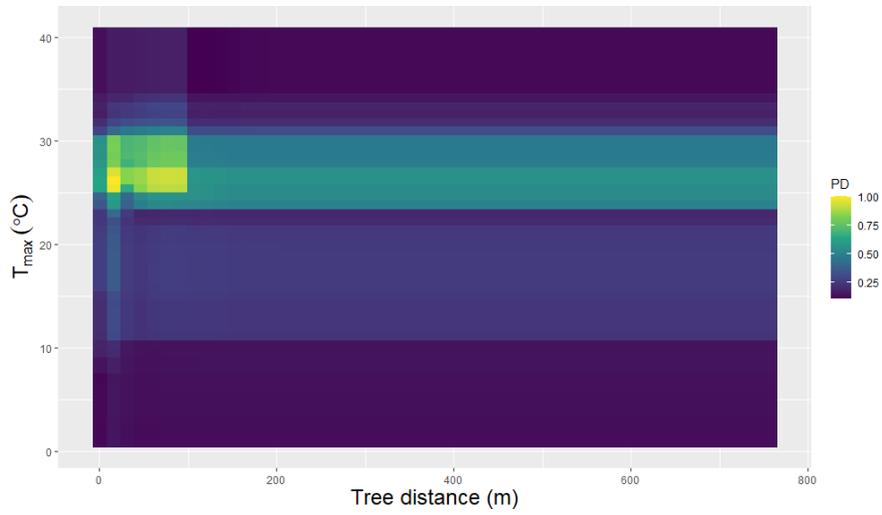
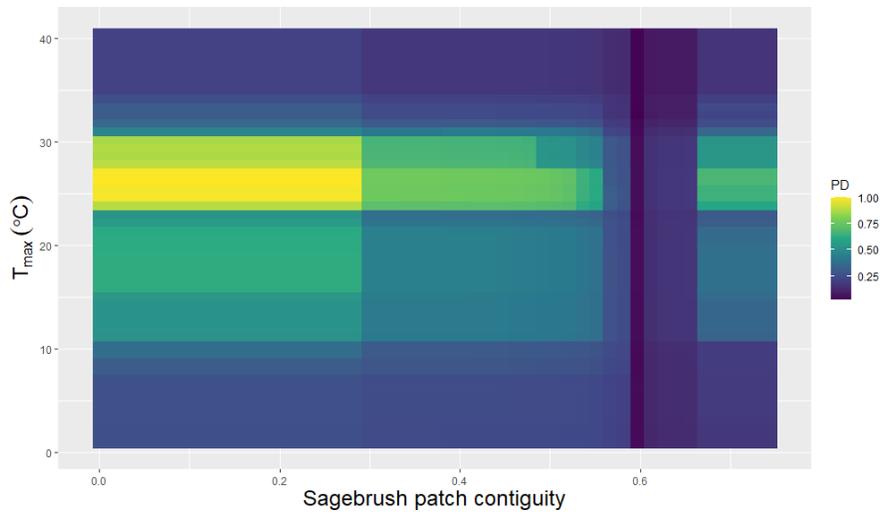


Figure 5. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to tree cover on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

a)



b)

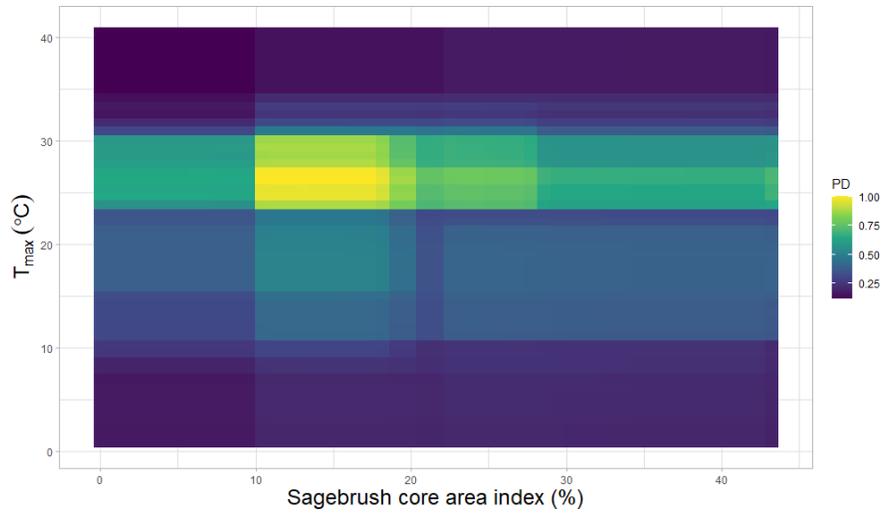


Figure 6. Marginal effects (partial dependence: PD) of average daily maximum temperature and **a**) sagebrush patch contiguity index (CONTIG) and **b**) sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

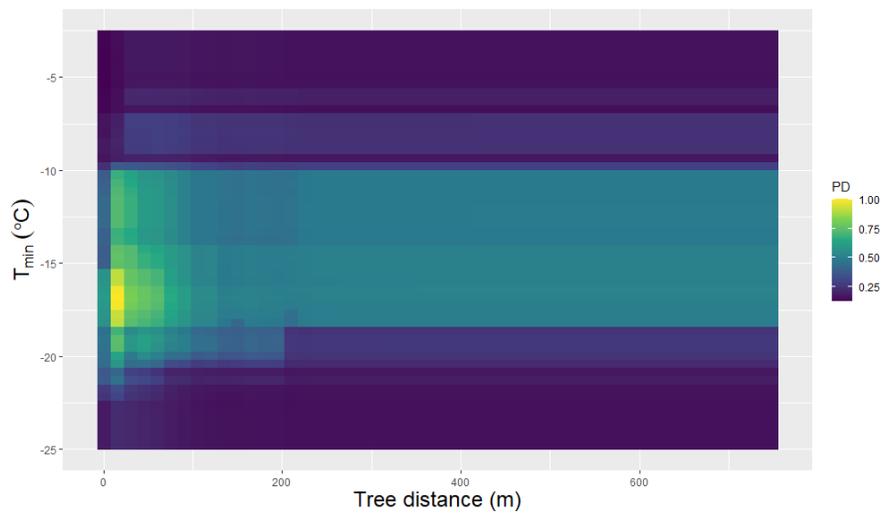


Figure 7. Marginal effects (partial dependence: PD) of average daily minimum temperature and distance to tree cover on sage-grouse habitat selection during winter in Buckskin Valley, Utah.

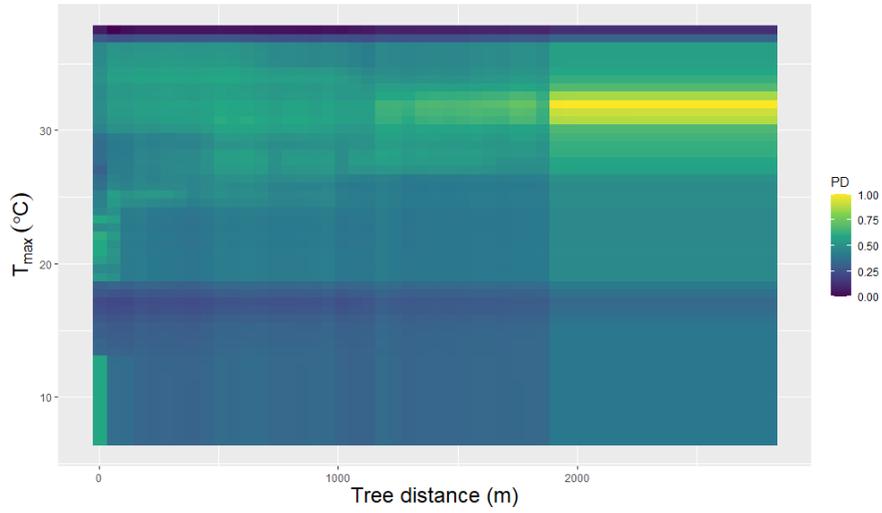


Figure 8. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to tree cover on sage-grouse habitat selection during summer in Steptoe Valley, Nevada.

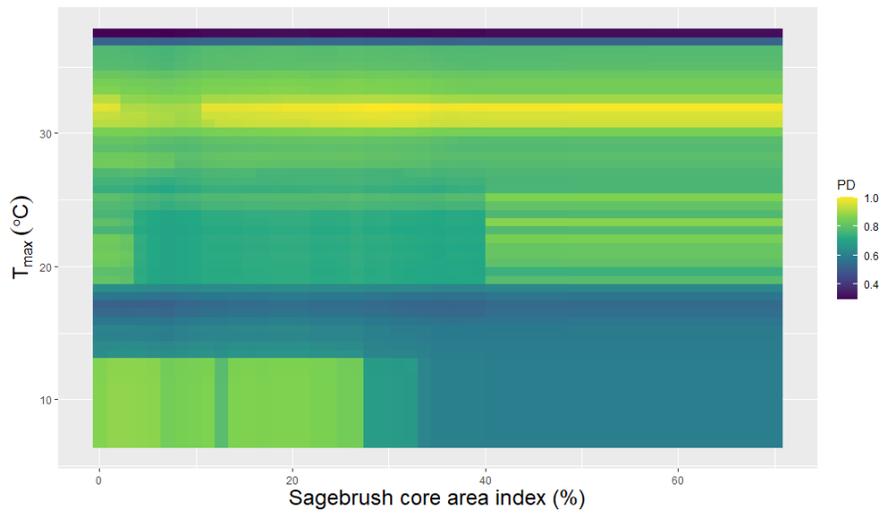
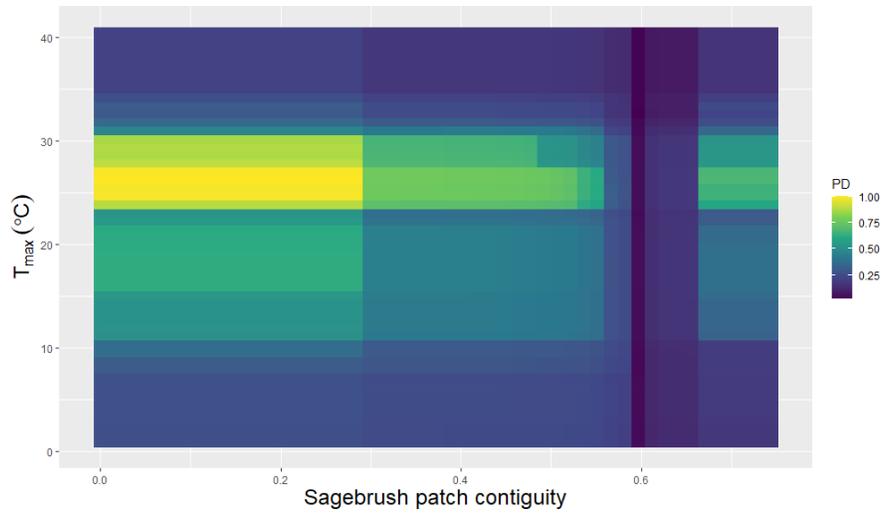


Figure 9. Marginal effects (partial dependence: PD) of average daily maximum temperature and sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Steptoe Valley, Nevada.

a)



b)

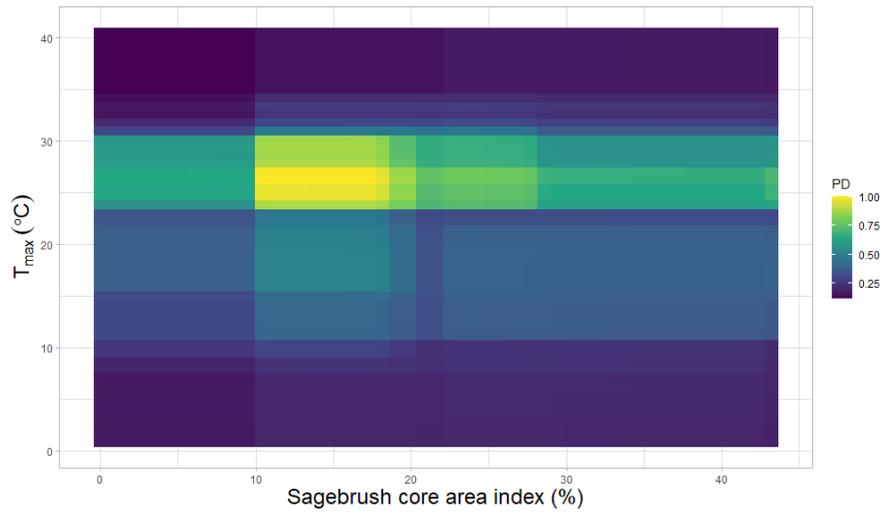
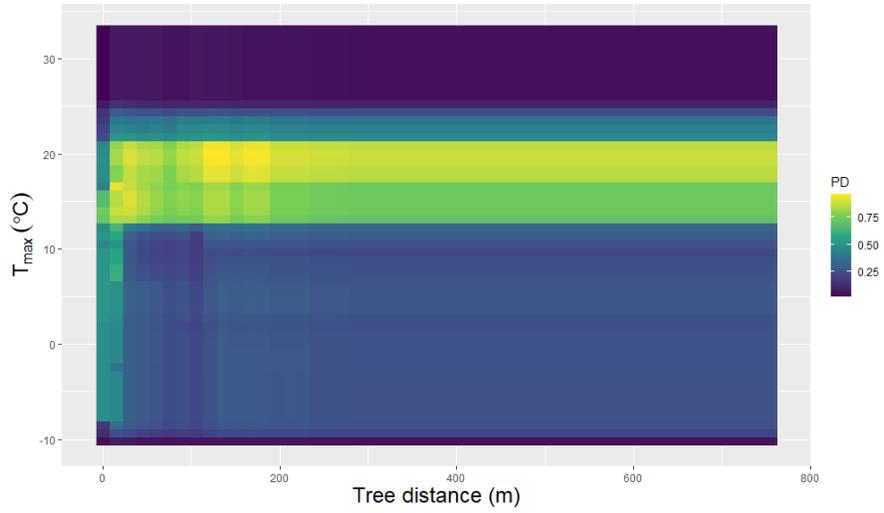


Figure 10. Marginal effects (partial dependence: PD) of average daily maximum temperature and **a**) sagebrush patch contiguity index (CONTIG) and **b**) sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

a)



b)

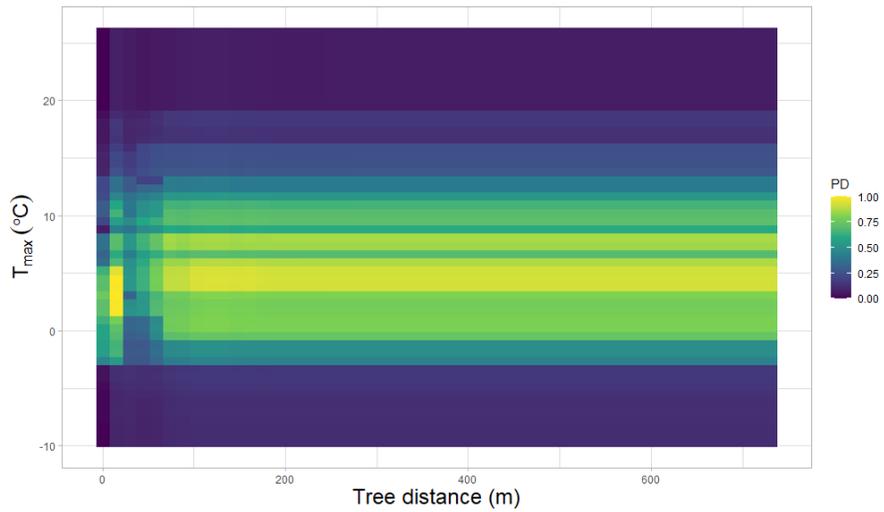
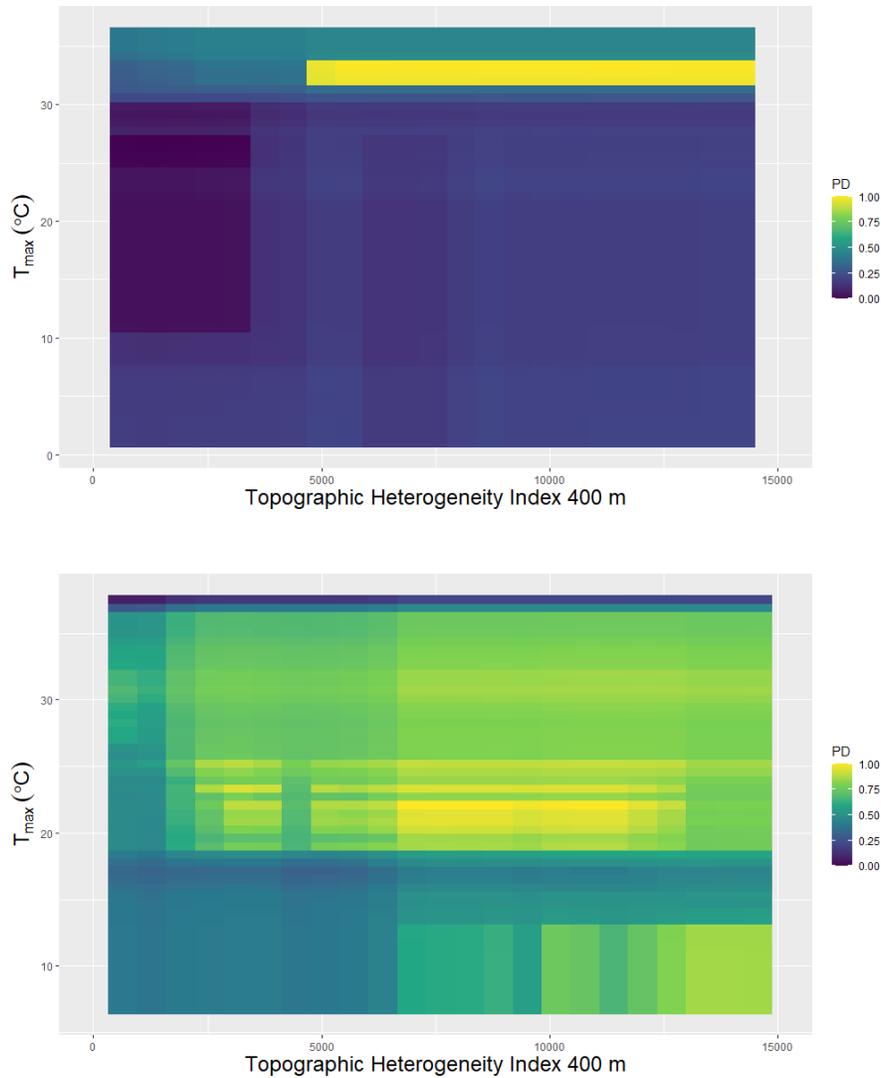


Figure 11. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to trees on sage-grouse habitat selection in Buckskin Valley, Utah during **a)** autumn and **b)** spring.

a)



b)

Figure 12. Marginal effects (partial dependence: PD) of average daily maximum temperature and topographic heterogeneity in a 400 m window on sage-grouse habitat selection during summer in a) Buckskin Valley, Utah and b) Steptoe Valley, Nevada.

COMPETING INTERESTS STATEMENT:

We declare no conflict of interest.

DATA ACCESSIBILITY 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.

AUTHOR CONTRIBUTIONS:

ATB led project development, contributed to sage-grouse capture, collected temperature data, and led data analysis and manuscript writing.

SNF acquired funding, contributed to project development, led sage-grouse capture, contributed to data analysis, and contributed significantly to manuscript writing and revising.

ACKNOWLEDGMENTS:

We acknowledge our many partners and supporters through many years of research. This work would not have been possible without the Utah Division of Wildlife Resources (UDWR), Utah State University (USU) Extension, S. J. Quinney College of Natural Resources (CNR) USU, Nevada Department of Wildlife (NDOW), U.S. Department of Interior Bureau of Land Management (BLM), and many research technicians and graduate students. Funding was provided by grants from NDOW and the BLM.