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Local and Regional Landscape Characteristics Driving Habitat Selection by Greater Sage-Grouse Along a Fragmented Range Margin

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LOCAL AND REGIONAL LANDSCAPE CHARACTERISTICS DRIVING HABITAT SELECTION BY GREATER SAGE-GROUSE ALONG A FRAGMENTED RANGE MARGIN

by

Aidan T. Beers

A dissertation submitted in partial fulfillment
of the requirements for the degree

of:

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in

Ecology

Approved:

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ABSTRACT

Local and Regional Landscape Characteristics Driving Habitat Selection by Greater Sage-Grouse Along a Fragmented Range Margin

by

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Utah State University, 2022

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Wildlife habitat selection analysis provides insight into some of the mechanisms limiting wildlife habitat at multiple scales and provides the means to effectively plan for wildlife conservation and management. This may be most important at range edges, where habitat tends to be of poorer quality and the factors limiting habitat suitability can be most apparent. In North America, sagebrush (*Artemisia* sp.) ecosystems and their denizens are among the systems most threatened by landscape changes. Among their residents are greater sage-grouse (*Centrocercus urophasianus*), sagebrush obligates that relies on intact sagebrush and face widespread threats to their persistence. The purpose of my research was to evaluate greater sage-grouse habitat selection along the southern edge of their distribution and the limitations to it in order to inform adaptive management at local and regional scales. In Chapter 2, I found that, despite the known risk of depredation due to tree cover, sage-grouse select habitat near trees, likely when they are able to exploit dense sagebrush and moderately rugged topography as visual cover from avian predators. In Chapter 3, I found that sage-grouse may be forced to balance the risks of depredation and exposure to thermal extremes, as they were most likely to select habitat near trees in the hottest areas of the landscape. I found that there is likely a threshold of temperature above which, if sagebrush provides inadequate thermal cover, sage-grouse may use the shade of tree cover to escape thermal stress. In Chapter 4, I evaluated the descriptive and predictive performance of random forest (RF) models and conventional resource selection functions (RSFs) for habitat selection. I found that RF consistently outperformed RSF in predicting new data, including across study areas, and revealed nonlinear effects and interactions undetected by RSFs. My research highlights the need for place-based sage-grouse and habitat management. My findings also demonstrate complications to our understanding of the threats they face, the factors limiting their habitat, and the best means by which to analyze habitat selection data.

(232 pages)

PUBLIC ABSTRACT

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Aidan T. Beers

In response to ongoing landscape change, wildlife species are likely to respond in varied ways. By studying habitat specialists, we are able to better understand the most likely ways in which the denizens of threatened ecosystems will react to those changes. Among the most threatened ecosystem types in North America are sagebrush ecosystems of the Intermountain West, where one of its most well-known residents, greater sage-grouse (hereafter, "sage-grouse), have lost more than 50% of their habitat due to fire, invasive species, climate change, encroachment by coniferous forests and avian predators using it, and human-caused landscape conversion. Sage-grouse rely on sagebrush throughout their lives, and there are ongoing efforts to protect them as emblems of vulnerable species and to preserve a changing landscape. The purpose of my dissertation, as part of the ongoing efforts, was to improve understanding of how sage-grouse select habitat along their southern distribution edge in southern Utah and Nevada, where habitat tends to be fragmented and of poorer quality. In this research, I used more than six years of location data from GPS transmitters on sage-grouse across four study areas to address how sage-grouse respond to the threats they face and by what means of data analysis we are best able to detect those threats and inform effective conservation. My research shows that, despite the risk posed by avian predators, sage-grouse in these study areas select habitat closer to trees than expected and do so when they are likely able to also use dense sagebrush cover and a rugged landscape to be concealed from predators. I also found that sage-grouse may use habitat near to trees for shade and escape from extreme heat and cold when the sagebrush in their habitat is not enough to provide shelter, suggesting that sage-grouse must often make risky decisions to balance the many threats they face. Finally, I found that random forests, an intuitive machine learning method, are able to detect important effects of sagebrush and tree cover on habitat selection, able to predict those effects in new areas, and should be considered among the useful and important tools for measuring wildlife-habitat associations.

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CHAPTER I

INTRODUCTION

DISTRIBUTIONS AND SCALE

Species distributions are delimited by the interaction of climate, topography, and interspecific relationships. Anthropogenic climate change is already impacting that interaction, changing ecosystems and driving impacts on species distributions (Walther et al. 2002a, Thomas et al. 2004b, 2006, Rull 2009, Chen et al. 2011b, Pecl et al. 2017, Bonebrake et al. 2018). Our ability to adapt to or manage these impacts will rely on our ability to understand and predict them. But there are significant gaps in our knowledge of species range shifts in response to climate change. These gaps include our ability to predict different rates of change that vary with topography and climate at multiple scales. Our lack of clarity around the potential responses is due in part to the uncertain role of microrefugia and behavioral plasticity across various scales (Mosblech et al. 2011, Ashcroft et al. 2012, Hannah et al. 2014, McCain and King 2014, McCain et al. 2016).

At local scales, it is difficult to predict climatic extremes and overall rates of change (Ashcroft et al. 2009, Ashcroft 2010, Hannah et al. 2014). This makes it doubly difficult to anticipate local and regional effects of climate change and to predict species redistributions or identify existing microhabitats (Crimmins et al. 2011, Hannah et al. 2014, McCain et al. 2016, Pecl et al. 2017). In order to address that issue, there is already useful research on the factors driving variability in topoclimate, the interaction between climate and topography that drives local-scale climatic conditions (Dobrowski 2011, Ashcroft and Gollan 2012, Ashcroft et al. 2012, Gollan et al. 2015, Morelli et al. 2016, Oyler et al. 2016). In addition to further refining our understanding of topoclimate, at what scales it can impact species, and where it may foster microrefugia, further research must address how land cover interacts with the impacts of thermal stress at local scales. There are likely many areas where a vulnerable wildlife may persist by exploiting suitable microhabitats through their behavior despite conditions becoming less suitable overall (Jeffress et al. 2013, Beever et al. 2017). Microrefugia are difficult to predict, but Pleistocene refugia played a strong role in shaping some modern distributions and current microrefugia are likely to play a similarly important role in species redistribution (Holderegger and Thiel-Egenter 2009, Mosblech et al. 2011, Ashcroft et al. 2012, Hannah et al. 2014). By identifying the environmental features driving species distribution and habitat selection at local scales, we are more able to predict and plan for changes in habitat configuration and connectivity.

Among the species vulnerable to these effects of landscape change at multiple scales across the western United States is the greater sage-grouse (*Centrocercus urophasianus;* hereafter 'sage-grouse'), a ground dwelling bird and a habitat specialist, dependent on the sagebrush of western North America (Connelly et al. 2004, Schroeder et al. 2004, Knick and Connelly 2011, USFWS 2013) that may be an indicator or "umbrella" species for sagebrush ecosystems (Hanser and Knick 2011, Copeland et al. 2014, Smith et al. 2019b, but see Carlisle et al. 2018). Despite being habitat specialists, sage-grouse demonstrate some plasticity in their habitat selection depending on their place within their distribution (Fedy et al. 2014, Doherty et al. 2016). This suggests that despite known threats, there are still cryptic idiosyncrasies in sage-grouse habitat selection at multiple scales, complicating our understanding of their habitat requirements in different areas of their distribution and of their likely response to ongoing change at regional and local scales.

SPECIES RANGE MARGINS

Delineating species ranges and their limitations is a central question in ecology with critical implications for conservation and management at species and ecosystem scales, spanning both basic and applied ecology. Species ranges are driven by both evolutionary and ecological factors, as their lineage, adaptive capacity, and climatic limitations interact with those of other species. Each species has evolved a fundamental niche, but its ability to fill that niche is limited by both the gradient of suitability within the niche and its competition with or reliance on other species.

At the simplest level, the fundamental niche is a product of evolution, established by a species' evolutionary history and its existing adaptive capacity (Bridle and Vines 2006). That includes the ability of a species to respond quickly to change, which is more likely to occur rapidly along distribution margins (Kirkpatrick and Barton 1997, Sexton et al. 2009). Populations at species' distribution edges are often more genetically isolated and have greater variability in individual and population level success than core populations, which can leave them more vulnerable to the impacts of rapid change and biological invasions (Hampe and Petit 2005, Sexton et al. 2009, Hannah et al. 2014). That variability and vulnerability could also lead to lower population density (Moilanen et al. 1998, Stewart et al. 2015).

The processes limiting species distributions are complicated by the mobility of wildlife and the varying capacity of species to shift their range in response to changing conditions at a variety of biologically relevant scales. For example, while the American pika (*Ochotona princeps*) is a habitat specialist that has been forced into increasingly high elevation, patchy, and isolated habitat by a changing climate (Beever et al. 2003, Grayson 2005, Wilkening et al. 2011), it is unclear to what extent and where they can exploit suitable microhabitat, as they persist in hot, dry sites like Craters of the Moon National Monument and below 1000 ft of elevation in the Columbia River Gorge (Simpson 2009, Rodhouse et al. 2010, Smith et al. 2019a). Consequently, new research has focused on the role that local processes have in shaping pika range and how it will respond to climate change depending on local context (Schwalm et al. 2016, Johnston et al. 2019, Smith et al. 2019a). Understanding that local context is especially important for wildlife at their range margins, where habitat tends to be of poorer quality, leaving populations less dense and more vulnerable to the effects of environmental and demographic stochasticity (Seabrook et al. 2014, Ruprecht et al. 2016). In almost all cases, a species' core distribution is where they are most suited to the climate and have the most positive and stable population increase; at the margins, there are more cases in which climatic variability can become limiting, habitat is more fragmented, and individuals are less able to find suitable refuge (Travis et al. 2004, Guo et al. 2005, Merrick and Koprowski 2017). There, they may have to rely on topoclimatic microrefugia, areas where local topography creates more stable conditions decoupled from regional trends or extreme weather (Thornthwaite 1953, Anderson et al. 2009, Rull 2010, Dobrowski 2011, Ashcroft et al. 2012).

The need to understand regional variation in habitat suitability is critical for conservation, including in greater sage-grouse (*Centrocercus urophasianus*). Doherty et al. (2016) demonstrated that habitat suitability and a species' fundamental niche must be understood hierarchically, from range-wide to regional to local scales. Additionally, other studies demonstrate biotic controls on the realized niche that are independent of climatic factors (Pearman et al. 2007, Jeffress et al. 2013, Schwalm et al. 2016). Nearing a range margin, species are more likely to be limited by competition with other species whose fundamental niche overlaps and may be more fit to that region. (Guo et al. 2005, Kaarlejarvi and Olofsson 2014). Poorer habitat quality and more vulnerable populations are evident near the edges of sage-grouse distribution. There, sagebrush gives way to other cover types, what suitable habitat exists is patchy, and sage-grouse are likely more vulnerable to extirpation (Herman-Brunson et al. 2009, Swanson et al. 2013, Rice et al. 2016, Walker et al. 2016, Lazenby et al. 2021). This has borne out in sage-grouse population trends—while populations have declined across their range, the trend has been most dire in areas near the edge of their distribution (Aldridge et al. 2008, Coates et al. 2021).

SPECIES DISTRIBUTION AND HABITAT SELECTION MODELS

The difference between fundamental and realized niches is demonstrated well by examining species distribution models (SDMs). SDMs can be a powerful tool for modeling species distributions and predicting changes over time (Pacifici et al. 2015). They can include both biotic and abiotic factors, but are often built with presence-only data to describe a species' bioclimatic envelope (Gomes et al. 2018). Using this presence-only data and macroecological variables is akin to mapping a species' fundamental niche, though usually will not cover it entirely because of the factors discussed above that would preclude presence data from its entire niche. However, SDMs tend to fail when they aren't validated with out-of-sample data and are less accurate at range margins (Capinha and Pateiro-López 2014, Vale et al. 2014). Where they ‘break down’ (i.e., exhibit a poor fit to the data) suggests limitations to the species’ ability to occupy that space caused by biotic interactions with other species more fit for that portion of the fundamental niche. Although there are some versions of SDMs that attempt a more mechanistic approach with physiological and spatial data (Kearney 2009), even those may fail to consider the ways in which biotic interactions impact the realized niche (Maguire et al. 2016). Instead, there needs to be an approach that more directly addresses the mechanisms driving wildlife associations with their habitat or incorporates communities to better account for biotic interactions like competition and facilitation (Balzotti et al. 2016, Maguire et al. 2016). For example, Balzotti et al. (2016) accounted for the fact that while sage-grouse are sagebrush (*Artemisia spp.*) obligates, the two species have independent fundamental niches. Both have macroecological constraints, but species of sagebrush persist well outside sage-grouse range while sage-grouse only rarely and seasonally use habitat with little to no sagebrush.

To more directly understand wildlife-habitat relationships, researchers often use resource selection or habitat selection analyses, which use some of the same statistical principles as SDMs while providing more insight into wildlife habitat by comparing the characteristics of animal locations to those of the environment available (Manly et al. 2002, Johnson et al. 2006, Lele et al. 2013, McDonald 2013, McDonald et al. 2013, Northrup et al. 2013). This kind of study can more precisely examine the features of the environment underpinning species distributions. Habitat selection analysis is based around that foundation of comparing used and available points. Even in its simplest form, resource selection functions (RSFs) provide valuable insights into wildlife habitat requirements and inform management decisions. Some of the different forms of analysis are used to address scenarios where hierarchical processes (Rolstad et al. 2000, Fieberg et al. 2010, Li et al. 2015, Muff et al. 2020) or nonlinear effects are present (Aarts et al. 2013, DeCesare et al. 2014, Severson et al. 2017a, Dahlgren et al. 2019, Kosicki 2020), a common problem in a complex system like ecology (Recknagel 2001, Cutler et al. 2007).

However, as a form of model-based inference RSFs have some limitations that have invited exploration into new methods of analyzing wildlife-habitat relationships, including several forms of machine learning to examine selection (McDonald et al. 2013, Cushman and Wasserman 2018, Shanley et al. 2021). Some of these methods have outperformed traditional methods and are gaining traction in wildlife habitat research (Elith et al. 2006b, Shoemaker et al. 2018, Valavi et al. 2022). Compared to traditional model-based inference methods, many machine learning techniques are more flexible and derive models from the data, allowing them to describe more complex relationships while not sacrificing predictive capacity (Recknagel 2001, Cutler et al. 2007, Olden et al. 2008, Valavi et al. 2022). Among these methods are random forests (RF), a nonparametric, tree-based method that aggregates weak-learning classification trees to form consensus model predictions (Breiman 2001). RF has been successfully implemented in wildlife-habitat analyses at multiple scales, and can be modified to be most appropriate for different questions and goals (Mi et al. 2017, Reisinger et al. 2021b, Shanley et al. 2021, Valavi et al. 2021). RF has already been used to analyze sage-grouse habitat associations, and will likely be a valuable tool in refining our understanding of sage-grouse habitat requirements and the ways in which it varies at local regional scales (Doherty et al. 2016, Severson et al. 2017b, Picardi et al. 2020). Though there is consensus on many of the habitat features that sage-grouse require, it is clear that limiting resources and specific thresholds in individual responses to them vary across sage-grouse distribution (Fedy et al. 2014, Coates et al. 2021). In order to best inform conservation and management, it is essential to understand the most important habitat factors at various scales and in different regions of sage-grouse distribution. By exploring newer, more flexible methods like RF, we may be better able to assess that variation and more accurately predict and plan for changes in habitat suitability and connectivity.

GREATER SAGE-GROUSE HABITAT AND CONSERVATION

The problems above point to a few questions to address essential knowledge gaps. How do climate, topography, and land cover interact to drive sage-grouse habitat selection at local scales? In vulnerable sage-grouse populations, how does the risk of thermal stress interact with the risk of predation to drive habitat selection? Further, what are the best means to assess sage-grouse habitat selection, especially in environments where we anticipate important thresholds and interactions?

Conservation concerns

Worldwide, shrubland ecosystems are among the most threatened due to changes in climate and land use (Wisdom et al. 2005, Romme et al. 2009, Staver et al. 2011, Miller 2020). In North America, sagebrush systems cover less than 50% of their former distribution, leaving sagebrush obligate species vulnerable to rapid range retraction, habitat fragmentation, and falling populations (West 1983a, Connelly et al. 2004). Sage-grouse have decreased in abundance by up to 90% since European settlement and by 80% since 1965 (Knick and Connelly 2011, Coates et al. 2021), with most of their decline directly linked to habitat loss (Braun 1998, Knick et al. 2003, Schroeder et al. 2004, Manier et al. 2013). They are often the focus of conservation efforts because of the myriad threats they face (Connelly et al. 2004, Aldridge et al. 2008, Knick et al. 2013), and there has been concern for their persistence for more than 100 years (Hornady 1916).

Among the most significant causes of sage-grouse habitat loss are land conversion and disturbance due to human activities like agriculture and energy development. Agriculture has been a major cause of sagebrush loss by land conversion and is commonly associated with sage-grouse extirpation (Aldridge et al. 2008, Wisdom et al. 2011). Similarly, livestock grazing is ubiquitous in current sage-grouse habitat and when not conducted appropriately can cause significant sagebrush reduction (Evers et al. 2013). As much as any other anthropogenic source, energy development (especially oil and gas) is a major threat to sage-grouse habitat (Knick et al. 2003, Aldridge and Boyce 2007, Holloran et al. 2010, Juliusson and Doherty 2017), with development concentrated mostly in Montana, Wyoming, and northern Colorado (Manier et al. 2013). Energy development has both direct and indirect impacts on sage-grouse and their habitat. First, constructing well pads, roads, pipelines, and transmission lines removes sagebrush and fragments otherwise intact landscape in some of the best remaining sage-grouse habitat (Walker et al. 2007, 2020, Doherty et al. 2008). Further, energy development and its associated infrastructure may also provide perches for avian predators and points of invasion for non-native plants (Connelly et al. 2000, Gelbard and Belnap 2003).

Throughout sage-grouse distribution, perhaps the most significant threat to their habitat is encroachment by conifers, especially pinyon-juniper forests (Wisdom et al. 2011, Baruch-Mordo et al. 2013, Coates et al. 2017, 2020). Like with energy development, conifer encroachment poses significant direct and indirect threats to both sage-grouse and their habitat. Increasing cover of pinyon-juniper forest reduces sagebrush, grass, and forb cover by direct competition, especially for water (Miller et al. 2008). In sagebrush ecosystems, increased tree cover also increases the chance of high intensity fire that could replace sagebrush with annual grasses (Chambers et al. 2014) and wildfire leads to sage-grouse population decline (Dudley et al. 2021). Further, areas encroached by conifers are more likely to experience soil erosion that could leave it untenable for sagebrush even if the trees were removed (Chambers et al. 2014). The problem of conifer encroachment is widespread in sagebrush habitats. As much as 90% of conifer expansion is into sagebrush habitat, where sagebrush cover is quickly reduced and sagebrush obligate species that require intact habitat can be excluded (Miller et al. 2000, Schroeder et al. 2004, Davies et al. 2011, Knick et al. 2013).

Conifers expanding into sagebrush are also a significant direct concern for sage-grouse because wooded habitats likely increase the risk of predation by avian predators. While only one study has directly shown greater sage-grouse mortality in areas of pinyon-juniper encroachment (Prochazka et al. 2017), sage-grouse also tend to avoid conifers and encroachment therefore restricts available habitat (Dinkins et al. 2017, Severson et al. 2017b). Predation as a whole may not be a limit to sage-grouse population growth across their range, though there is considerable evidence that ravens, a threat mostly to sage-grouse nests, can be a strong limiting factor in marginal and fragmented habitats (Gregg et al. 1994, Bui et al. 2010, Coates and Delehanty 2010, Dinkins et al. 2014). In some parts of sage-grouse range, concern is focused especially on the impact of ravens, which have expanded their range in recent decades due to increased human structures and conifer encroachment (Coates et al. 2016a) and represent a threat to sage-grouse nests and broods (Dinkins et al. 2016). In response to the threats caused by conifer encroachment, there has been effort in affected parts of sage-grouse distribution to remove trees, which has largely resulted in more suitable habitat and benefits to local populations (Frey et al. 2013, Severson et al. 2017c).

Climate change implications

Many of these risks to sage-grouse and their habitat may be compounded by climate change, as sagebrush communities are replaced and fragmented because of climate-induced precipitation and fire regime shifts (Snyder et al. 2019). One study found that climate change is likely to worsen the impacts on sage-grouse of conifer encroachment, as the encroached landscape retains water poorly and is likely to leave downstream areas without water earlier than they tolerate (Kormos et al. 2017). For a sagebrush obligate like sage-grouse, this could be catastrophic, especially at the southern end of their range where habitat is already fragmented and climate change is predicted to reduce sagebrush cover (Kleinhesselink and Adler 2018, Renwick et al. 2018). Existing work also demonstrates the negative impact of direct thermal stress on other gallinaceous birds (Hovick et al. 2014, Tanner et al. 2017), and has suggested the same is likely true for sage-grouse (Blomberg et al. 2012, Gibson et al. 2017).

RESEARCH OBJECTIVES

Sage-grouse have been the subject of considerable research and conservation efforts for several decades and the threats to their persistence are well established (Braun et al. 1977, Braun 1998, Knick and Connelly 2011). However, that extensive research has also highlighted areas meriting further nuance and investigation. My research will fill some of these gaps in understanding, focusing especially on how different factors of topography, land cover, and climate impact sage-grouse habitat selection and populations.

Because sage-grouse are likely threatened across most of their range, some research focuses on describing those threats and habitat selection at broad scales to provide actionable science to as many stakeholders as possible (Aldridge et al. 2008, Garton et al. 2011, Row et al. 2018). That work is invaluable. However, to best conserve and manage sage-grouse at local scales, where most decisions are made, it is essential to identify fine-scale environmental factors driving habitat suitability and habitat selection. Further, it is important to understand how those fine-scale impacts vary across broad scales and how different macroecological conditions change sage-grouse habitat selection (Doherty et al. 2016, Picardi et al. 2020). For example, though sage-grouse tend to avoid trees because of the risks they pose, there are many areas of sage-grouse range with little to no tree cover. In those areas, it would be ecologically meaningless to include the impacts of trees in conservation and management, as sage-grouse decisions are driven by other features. For that reason, it is important to develop place-based models that account for both the local and regional environment. In this thesis, my goal was to analyze the impacts of land cover and topography on sage-grouse habitat selection and how those impacts vary across study areas at the southern edge of their distribution. Further, I assessed the potential role of exposure to thermal stress in sage-grouse habitat selection. The habitat of that southern range edge is fragmented, of poorer quality than the core of sage-grouse distribution, and likely to face effects of climate change. Sage-grouse there may therefore be forced to account for thermal stress in their environment. Lastly, I explored new methods of habitat selection analysis and their capacity to both predict new data and provide more precise, actionable information to guide conservation than conventional methods.

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CHAPTER II

GREATER SAGE-GROUSE HABITAT SELECTION VARIES ACROSS THE MARGINAL HABITAT OF ITS LAGGING RANGE MARGIN

ABSTRACT

Studying wildlife-habitat relationships at the edges of their range can provide valuable insights into the environmental factors limiting wildlife distributions and most likely to drive extirpations and range shifts in response to landscape change. Yet the relative impact of those factors is likely different along the range margin, so it is important to identify limitations to suitable habitat at both regional and local scales. Some of the most drastic impacts of large-scale landscape changes in North America have occurred and are forecasted in the sagebrush ecosystems, where species unable to seek new habitat in the fragmented landscape will be vulnerable to climatic extremes, vegetation community shifts, and anthropogenic land use change. One of the species likely under major threat from landscape changes is the greater sage-grouse (*Centrocercus urophasianus*), a sagebrush obligate with habitat constraints that make it susceptible to habitat loss impacts as sagebrush systems contract and fragment at their southern range margin, already naturally fragmented. In this study we evaluated factors of topography and land cover directly impacting habitat selection by sage-grouse in four study areas along their lagging range edge. We used >116,000 GPS locations from >90 grouse across four study areas in southern Utah and Nevada from 2014-2020 in habitat selection analyses using random forest models. Our results showed that sage-grouse exploit topography and sagebrush cover, possibly to break predator sight lines and moderate the risk posed by avian predators using tree perches, complicating the effects of

tree cover and conifer encroachment into sagebrush habitat. We found similar trends across all four study areas, suggesting sage-grouse along the southern range margin face similar limitations. However, the effects were nonlinear and varied—models trained in one study area were only moderately successful at predicting selection in others. The local idiosyncrasies along this southern range margin indicate a need for place-based conservation for sage-grouse and other potentially imperiled species. Incorporating new understandings of local impacts will refine regional and range-wide models and support efforts to effectively create habitat and plan for range shifts by vulnerable species in response to environmental change.

INTRODUCTION

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

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

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

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

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

METHODS

Overview

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

Study region

Our study region included several discrete areas of sage-grouse habitat along or near their southern range margin in southern Utah and Nevada. In Utah, that included the

Panguitch, Bald Hills, and Hamlin Valley Sage-Grouse Management Areas (SGMAs: Utah Public Lands Policy Coordination Office 2019). Sage-grouse habitat in this region tends to be fragmented at large scales by Basin and Range province mountains. In Nevada, we worked in the northern end of Hamlin Valley within the Lincoln population management unit (PMU) and the Steptoe/Cave PMU (Emm et al. 2019) (Figure 2.1). The total study region spanned 37.2 - 39.1°N latitude and 112.4 - 114.9°W longitude. Elevation across the entire area ranged from 1600 m to 2800 m. During the study period, our study areas had an average temperature of 8.0 °C in Panguitch, 8.1 °C in the Bald Hills, 10.3 °C in Hamlin, and 7.4 °C in Steptoe/Cave. The study areas received an average of 378 mm in Panguitch, 350 mm in Bald Hills, 302 mm in Hamlin, and 277 mm in Steptoe/Cave (PRISM 2020).

Each of the valleys in our study area was dominated to varying degrees by species of sagebrush (*Artemesia sp.*). In the most xeric valleys, sagebrush species accounted for more than 90% of vegetation, interspersed with bare ground and sparse grasses and forbs. In more mesic areas, native bunchgrasses, rabbitbrush (*Ericameria sp.*), and a variety of forbs were present, though sagebrush was still the dominant shrub species. The sagebrush was mostly *A. tridentata wyomingensis* and other *A. tridentata* subspecies, with *A. nova* common in the more xeric habitats. Our study region represented much of the range of conditions prevalent in the Great Basin-Colorado Plateau sagebrush semi-desert, a subset of the Intermountain West region, but generally more xeric than much of sage-grouse range (West 1983b). Across the study region, the valleys were fringed with mixed woodlands of pinyon pine and juniper while higher elevations areas included quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), mountain mahogany

(*Cercocarpus sp.*), juniper, spruce (*Picea sp.*), and fir (*Abies sp.*). There were also some high elevation sagebrush patches used by sage-grouse that migrate to upward during the summer. In each study area, some sage-grouse relocate seasonally while others do not apparently dramatically change their home range.

Data collection

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

Transmitters were programmed to collect 4 GPS locations per day: dawn, mid-day, dusk, and night. During data processing we removed points from the dataset that were acquired from any individual with fewer than 100 successful fixes or collected within 48 hours post-release. After also removing erroneous points that were clear outliers, our dataset included 116,310 points from 96 individuals (median n=1398/individual) during the period of 2014-2020. Of those 96 sage-grouse, 31 were in Bald Hills (43,449 locations), 12 were in Cave (10,375 locations), 29 were in Hamlin (44,950 locations), and 24 were in Panguitch (17,536 locations). We estimated individual 90% home ranges using a kernel density estimator with the default settings from the R package *adehabitatHR* (Calenge 2017) and examined the habitat within those estimated home ranges to evaluate third-order selection (Johnson 1980).

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

Environmental covariate data

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

We downloaded elevation data for the extent of our study region at 10 m resolution using the R package *elevatr*, which accesses Amazon Web Services (Hollister et al. 2017). From that digital elevation model (DEM) we calculated metrics of topographic position, heterogeneity, and slope. Topographic position index (TPI) is calculated as the relative elevation of any one cell compared to the cells around it within a user-specified window size, showing whether a DEM cell is part of a hill, valley, or flat ground (Jenness et al. 2013). We also calculated a topographic heterogeneity index (THI) by summing the absolute value of TPI within that same window size for a measure of overall ruggedness. We calculated TPI and THI each at window radii of 50, 200, and 400 m. More information about the values of environmental covariates for each study area are available in Supplementary Information (Appendix S1: Table 2.1).

Model development

We built models within each of the four study areas to evaluate regional variation. We also split the data into three seasons: Breeding (March – May), Summer (June – September), and Fall/Winter (October – February), resulting in models for each season and models across all seasons. Though seasonality was not our primary focus, it is well established that sage-grouse require different seasonal habitats (Connelly et al. 2000, Dahlgren et al. 2016). Including season as part of the analysis allowed us to detect possible effects of seasonality on our other findings and make more precise evaluations. We analyzed the sage-grouse habitat selection using random forest models (RF), a tree-based ensemble machine learning classifier (Breiman 2001). RF is a nonparametric method that builds hundreds or thousands of classification trees, each using a bootstrap sample to train the model while a subset is withheld as an out-of-bag testing dataset for each finished tree in the forest. Compared to the more commonly used resource selection function (RSF), RF is better able to detect nonlinear effects, is less prone to problems of autocorrelation because it does not assume independence of samples, and by default considers interactions among variables (Breiman 2001, Cutler et al. 2007, Biau 2012, Farrell et al. 2019). It has been successfully used to model species distributions and animal habitat selection (Evans and Cushman 2009, Carrasco et al. 2014, Doherty et al. 2016, Schwalm et al. 2016, Shoemaker et al. 2018, Zhang et al. 2019). RF includes in its process withholding a subset of data to test the trained classification trees, but we took additional steps to ensure thorough model training and validation. First, we created a randomly assigned training dataset with which to develop models using 70% of the data within each season and study area. We used the R package *ranger* (Wright and Ziegler 2017) to build RF models using leave group out k-fold cross validation (LGOCV) with the data grouped by individual sage-grouse ID to strengthen the model's internal evaluation process and avoid overfitting. In each of folds, the data were divided by using three quarters of the individuals' data for model training and the remaining for the cross validation. To further avoid overfitting, we increased the minimum node size in each tree of the RF from the default of 1 for RF classification to either 20 or 50 points in model tuning. We also tuned the models by allowing the number of variables randomly selected for evaluation at each node (*mtry*) to vary between 3, 4, 5, and 8, whereas the default is the square root of the total number of covariates. We selected the best overall model by model accuracy. In both classification analyses such as RF and in presence-only models like RSF, it can be problematic to oversample from one class of the response variable (Chen et al. 2004, MacKenzie 2005, Boyce 2006). Therefore, for each study area – season combination, we randomly sampled from the available points for each individual for comparison with GPS point detections for that individual, so that each model had a 1:1 used-available ratio and avoided the problems of an imbalanced design (Evans and Cushman 2009, Cushman et al. 2010, Valdes-Donoso et al. 2017). We repeated that sampling process without replacement until all 'available' points were included in models and averaged the models' predictions during model evaluation (similar to Khalilia et al. 2011).

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

Comparison with RSF

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

Model validation

After training and selecting the best fitting models using RF, we evaluated model performance in predicting the withheld 30% of the dataset true skill statistic (TSS). TSS can theoretically range from -1 to 1, with 0 being a totally uninformative model. Because there is argument that metrics like TSS may be inappropriate for a habitat selection study (Johnson et al. 2006, Fieberg et al. 2018), we also included the model's Sensitivity. In addition to those evaluation metrics, we also built calibration plots for each of the models, calculating the correlation between expected and observed probability of selection, where a higher correlation indicates better model performance (Fieberg et al. 2018). We repeated the model validation process for each iteration of every study area – season model combination and recorded the average by each metric.

Study area comparison

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

RESULTS

The presence of trees influenced sage-grouse selection among the study areas, but differently for each area. In all four study areas, linear distance to trees (TREEDIST), the density of trees at 800 m (TREEDEN800), or the density of trees at 400 m (TREEDEN400) were among the most important variables influencing sage-grouse selection, as measured by mean decrease in Gini score (Table 2.2). In each study area there was a clear negative effect of TREEDEN800 (Figure 2.2a) and TREEDEN400 (Figure 2.2b), as sage-grouse selected for low tree density. This effect was nonlinear and for each study area there were different rates of change in selection across tree density.

For example, in the Bald Hills area sage-grouse selection was about < 1% more likely at 15% tree cover (TREEDEN800) than predicted by the rest of the Bald Hills dataset, while in Panguitch at the same level of tree cover sage-grouse selection was 8% *less* likely. However, in all study areas there was selection for landscape with < 4% tree cover, an overall trend of decreasing selection with increased tree cover, and a negative association with proximity to trees in all study areas but Panguitch (Figure 2.2c). In each study area, tree cover between 30% and 40% was associated with less pronounced avoidance (though still not selection) compared with higher or somewhat lower cover.

Our results demonstrate important roles of topography and sagebrush cover, including in changing or moderating the negative impact of trees. Topographic Heterogeneity Index at 400 m (THI400) was consistently one of the most important variables in the models. Most importantly, sage-grouse selected slightly heterogeneous terrain over flat or more rugged terrain in the Bald Hills, Cave, and Panguitch study areas as measured by THI400 (Figure 2.3a). Similarly, sage-grouse selected terrain that is slightly lower in elevation than the surrounding area within a 200 m window and tended to avoid high points or very low points in the Cave, Hamlin, and Panguitch study areas (Figure 2.3b). We found that slope was often important (among the top six variables in ten of twelve study area – season model combinations) but it was always less influential than at least one other topographic variable (e.g., TPI, THI) based on mean decrease in Gini score (Table 2.2). Slope had a generally negative relationship with sage-grouse habitat selection, though its effect was uneven (Figure 2.3c). Two-way partial dependence plots further demonstrated the influence of topography on selection. For any given distance to trees, sage-grouse habitat selection was most likely in moderately heterogeneous terrain and in slightly low-lying, protected areas (Figure 2.4a).

Further, the RF models suggest that sagebrush cover plays a role in moderating the impact of TREEDIST. Sagebrush patch Core Area Index (CAI) and patch contiguity (CONTIG) were among the least important variables in the RF models, but two-way partial dependence plots illustrated their impact; for any given distance to trees, sage-grouse selection was more likely in areas of higher CAI (Figure 2.4b) and CONTIG (Figure 2.4c).

Seasonality

Predictive power was greater when the models were built with data from only one season (Table 2.3), suggesting that within each season, sage-grouse have differing habitat selection criteria. In each season, sage-grouse selection decreased as tree density within 400 m increased (TREEDEN400: Figure 2.5b). This effect was strongest in the Fall/Winter season and weakest in the Breeding season. In each season there was a positive influence on selection at low tree cover; birds selected areas with < 2% cover in Summer and Breeding seasons and < 11% in Fall/Winter, which we found by calculating local minima in feature contribution. Selection for distance to trees in each season had a nonlinear effect. In Breeding and Fall/Winter seasons, sage-grouse avoided areas close to trees, but in Summer they selected areas close to trees and avoid areas very far from trees (Figure 2.5c).

There was a mixed effect of sagebrush core area among the seasons; with increasing CAI, this factor’s contribution to modeling habitat selection increased for the breeding and fall/winter seasons, with positive effects above moderately high CAI values;

this effect was not present for the summer season (Figure 2.6a). Sagebrush contiguity (CONTIG) similarly influenced habitat selection in the Breeding and Fall/Winter seasons with positive effects above a value of 0.75 (Figure 2.6b). During the summer, sage-grouse selected for moderate sagebrush continuity (0.4 < CONTIG < 0.75) but avoided very contiguous sagebrush (> 0.75). That seasonal variation in sagebrush impacts was also somewhat consistent across study areas (Figure 2.7). Most notably, there was increasing rate of selection in all four study areas during the Breeding season at high CONTIG values (> 0.75), but strong avoidance of those same areas during Summer in three study areas. In the fourth, Panguitch, there was still a peak in selection at around the same CONTIG value, but very weak selection above that.

The effect of topography also varied seasonally. Most notably, during the Breeding season sage-grouse selected most for moderately heterogeneous terrain in all study areas but the Bald Hills, while in Summer sage-grouse avoided the moderate terrain and selected either very flat or rugged terrain everywhere but in Panguitch (Figure 2.8). In Fall/Winter, the peak of selection in each study area was in terrain of low to moderate heterogeneity more than either the least or most rugged terrain.

Model performance

Within each study area, the RF models consistently performed well when predicting withheld data measured by each evaluation metric (Table 2.3). The TSS for RF models ranged from 0.579 to 0.767 indicating fairly strong predictive performance (Landis and Koch 1977). Model Sensitivity values (proportion of true locations correctly predicted) were also high, ranging from 0.811 to 0.966. The RF models consistently performed better than the RSF models when predicting withheld data and predicting data from other study areas. The RSF models were weaker predicters though still somewhat informative, with TSS values from 0.229 to 0.431 and Sensitivity from 0.668 to 0.782.

Used-habitat model calibration also demonstrated moderate to strong model predictive performance (Table 2.3). The lowest calibration correlation coefficient among all study area – season model combinations was in Cave Valley in Summer, with an average correlation across iterations of 0.811, while the highest was in the Bald Hills in Breeding season at 0.934.

DISCUSSION

Model performance

The RF models performed very well within study areas and even the model including all study areas and seasons had strong predictive power (TSS = 0.579). The RF model including all study areas was not as accurate as any single study area – season combination model (TSS range = 0.603-0.767; Sensitivity range = 0.825-0.966), though the most important variables in each study area were similar. Distance to trees or tree density within 800 m were always among the most important, as was THI400, one of the factors that likely moderates the impact of predation risk due to trees. The failings in predictive power across study areas may derive from a difference in the magnitude and thresholds of the driving variables. For example, increasing TREEDEN400 in every study area had a generally negative effect on selection, though nonlinearly and with different local perturbations.

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

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

Regional variation

Our findings reinforce the fact that range-wide predictions must account for regional and local drivers of habitat selection. The results of our study suggest that sage-grouse experience different limitations and drivers of habitat selection throughout their range; across this southern range margin topography plays a stronger role than previously described for any part of their range. In more contiguous sagebrush semi-desert or sagebrush steppe habitat, topography was less influential than demonstrated in this study (Doherty et al. 2008, Knick et al. 2013), similar to the findings of Walker et al. (2016), who documented sage-grouse selection for somewhat rugged terrain in a naturally fragmented area, especially in winter. Doherty et al. (2016) showed that the most important ecological variables were markedly different across regional sage-grouse management zones. In our study, we worked within only one management zone and further demonstrated the "idiosyncrasies of place" (Jeffress et al. 2013) that are important to evaluate at several scales. We suspect that in areas of sage-grouse range where conifer encroachment is less pervasive, sage-grouse are less likely to exploit topography for shelter from predation.

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

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

Seasonality

Many previous studies have found seasonal variation in sage-grouse habitat requirements. Our data support these past studies; within any study area or across all four, the greatest predictive performance was in models of one season rather than the whole year. Our study reaffirms some of the seasonal components to selection previously described, including a greater affinity for large areas of sagebrush and generally less heterogeneous terrain in winter than in summer (Doherty et al. 2008, Carpenter et al. 2010). However, the effect was nonlinear, and sage-grouse during Summer in all four study areas and during Fall/Winter in all but Hamlin avoided the most contiguous sagebrush patches (Figure 2.8), which may offer inadequate thermal cover or food resources during these times. We found that as distances farther than 1000 m from trees, sage-grouse selection became less likely during Summer and in each study area there was a generally decreasing probability of selection with increasing distance to trees (Figure 2.5). This may be because in our relatively xeric study areas, mesic resources necessary to survive the summer (Drut et al. 1994) are less likely to be found where there is too little water for trees to persist (West 1983b). It may also be that sage-grouse along this southern range margin use areas with trees in summer as thermal cover, despite the predation risk, especially when they can also exploit topography for visual cover, as we found that selection during Summer for the most rugged terrain tended to be higher than for moderately heterogeneous terrain (Figure 2.8).

Conclusions

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

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

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TABLES AND FIGURES

Table 2.1. All predictor variables used in data analysis. Land cover variables are at 30 m horizontal resolution and terrain variables are at 10 m horizontal resolution.

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

Table 2.2. Top six most important environmental variables in each study area – season model combination, measured by mean decrease in Gini impurity index.

Study Area	Season	Important Variables
Bald Hills	Breeding	TREEDIST, TREEDEN800, TREEDEN400, THI400, THI200, Slope
Bald Hills	Summer	TREEDEN800, THI400, TREEDIST, TREEDEN400, THI50, THI200
Bald Hills	Fall/Winter	TREEDIST, TREEDEN800, THI400, TREEDEN400, THI200, THI50
Cave	Breeding	TREEDEN800, THI400, TREEDIST, THI200, Slope, TREEDEN400
Cave	Summer	TREEDIST, THI400, TREEDEN800, Slope, TREEDEN400, THI200
Cave	Fall/Winter	TREEDIST, THI400, TREEDEN800, Slope, THI200, THI50
Hamlin	Breeding	THI400, TREEDIST, TPI400, THI200, Slope, TPI200
Hamlin	Summer	THI400, TREEDIST, THI200, Slope, TPI400, TREEDEN800
Hamlin	Fall/Winter	TREEDIST, THI400, THI200, TREEDEN800, TPI400, Slope
Panguitch	Breeding	TREEDEN800, TREEDIST, THI400, TREEDEN400, Slope, THI200
Panguitch	Summer	TREEDEN800, THI400, TREEDEN400, THI200, Slope, TPI400
Panguitch	Fall/Winter	THI400, TREEDEN800, Slope, TREEDEN400, THI200, TPI400

Table 2.3. RF model performance measured by true skill statistic (TSS), proportion of used points correctly predicted (Sensitivity), and used-habitat calibration correlation in each study area and each season.

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

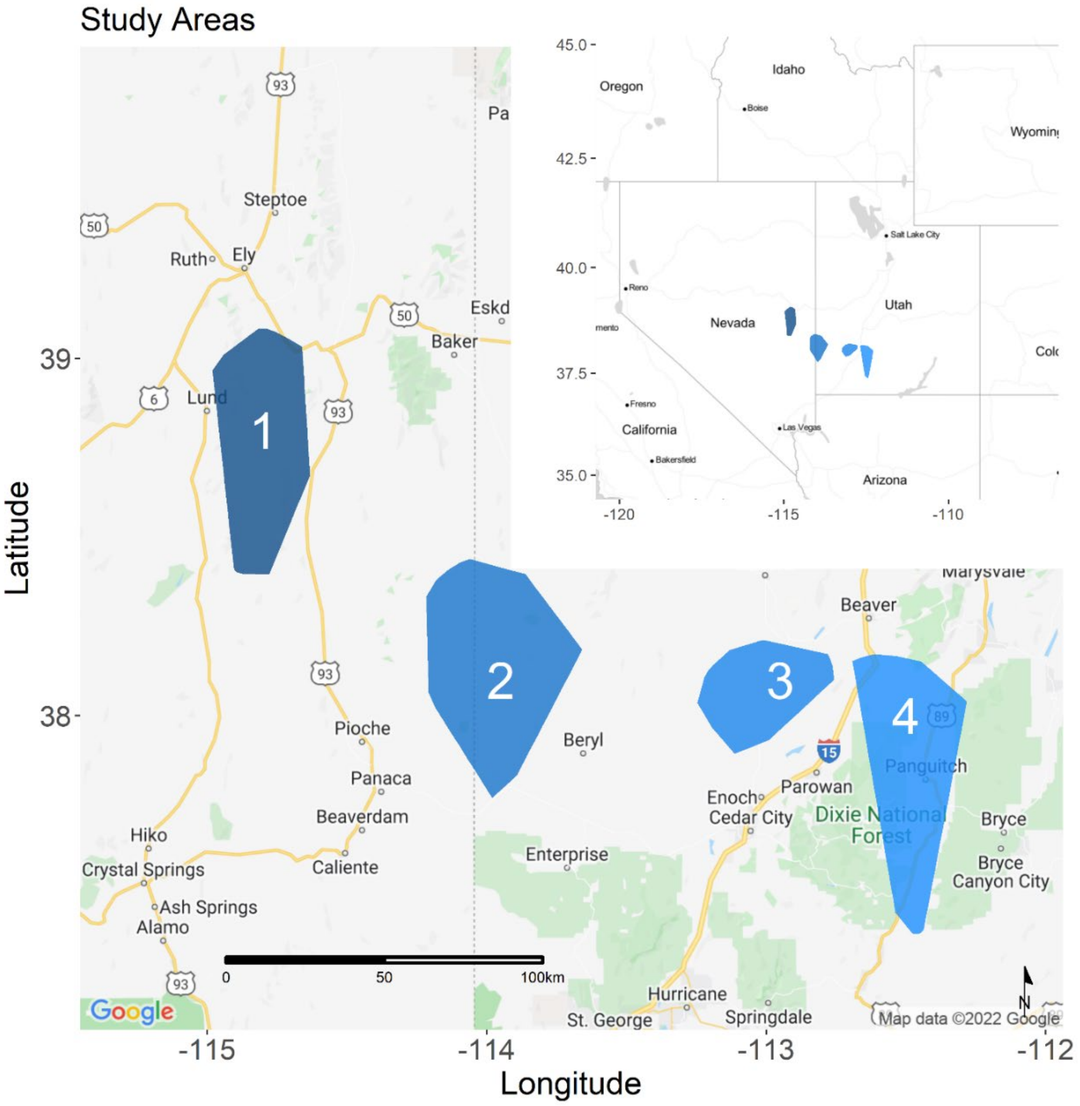

Figure 2.1: Four study areas and their context in Utah and Nevada, drawn here by a minimum convex polygon around the data points used in our analyses. Study areas are 1) Cave/Steptoe Valleys, 2) Hamlin Valley, 3) Bald Hills, and 4) Panguitch.

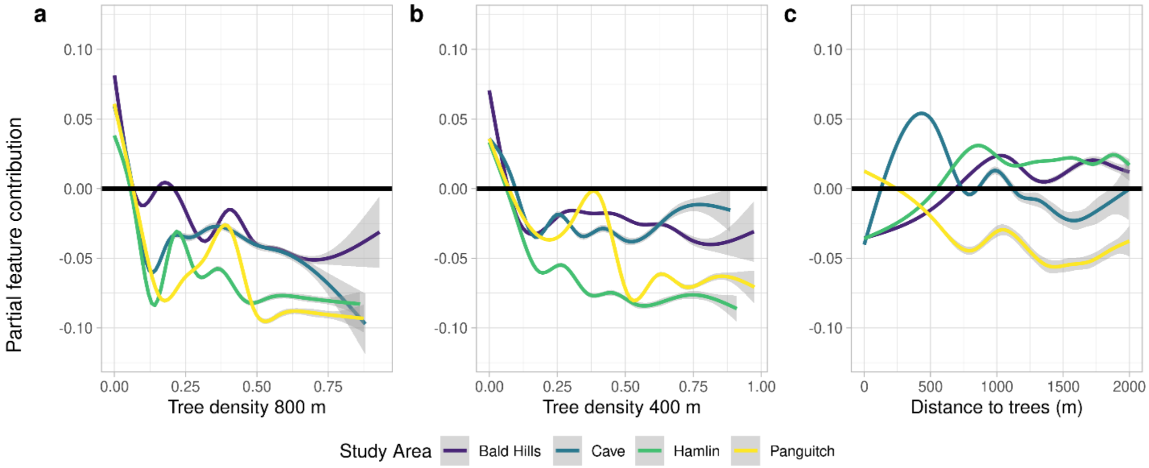

Figure 2.2. Feature contribution[1] of three variables of tree cover in models across four study areas. Panel a) shows the contribution of density of treed pixels in an 800 m radius (TREEDEN800), panel b) shows the contribution of density of treed pixels in a 400 m radius (TREEDEN400), and panel c) shows the contribution of the distance to trees (TREEDIST).

[1] Feature contribution measures how a variable impacts the random forest model's prediction of a point's used vs available status at each value of that variable. A positive value indicates a greater probability of the point being "used" compared to the prediction made by the rest of the model. The solid black line at feature contribution = 0 indicates the point at which selection and avoidance are equally likely.

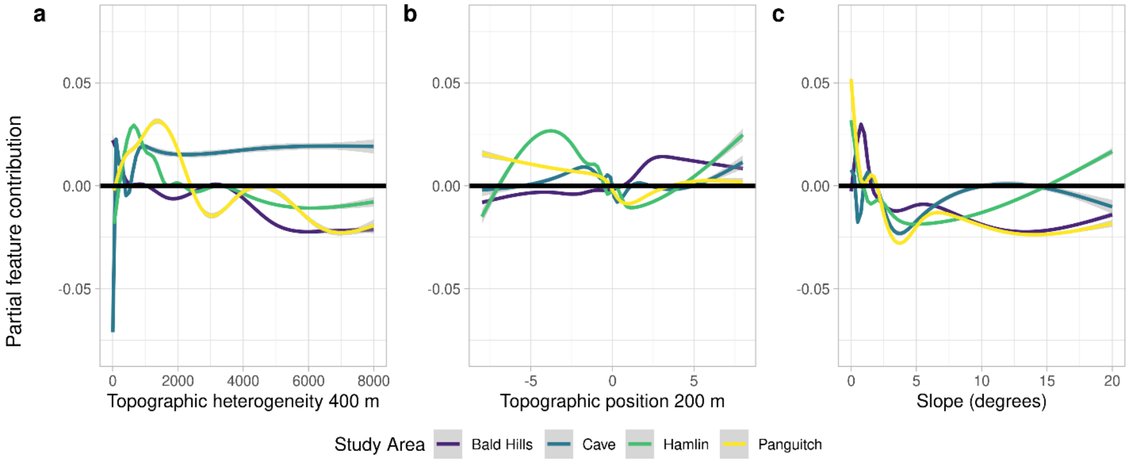

Figure 2.3. Feature contribution of three topographic variables in the models across four study areas. Panel a) shows the impact of topographic heterogeneity within a 400 m radius (THI400), panel b) shows topographic position compared to a 200 m radius (TPI200), and panel c) shows topographic slope.

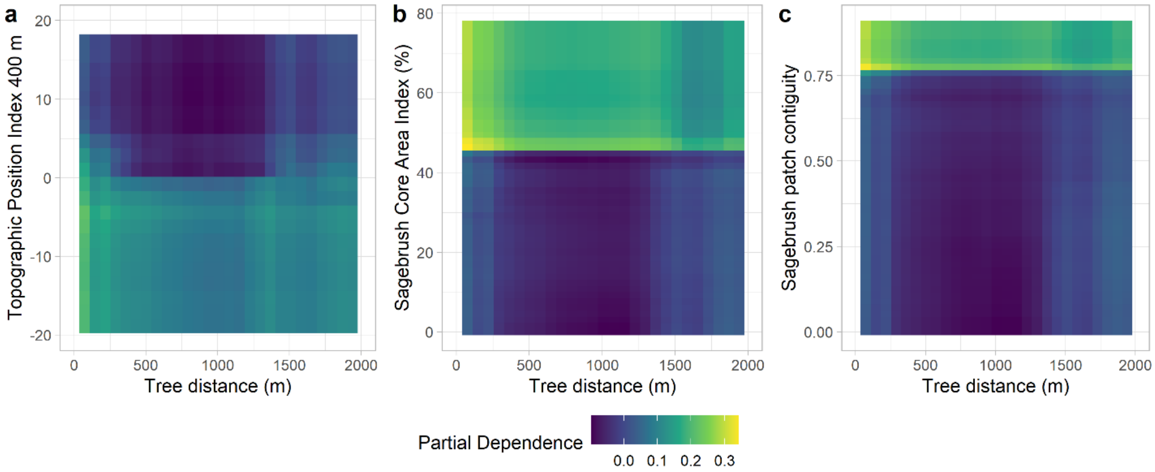

Figure 2.4. Partial dependence[1] of a) topographic position index within a 400 m radius (TPI400), b) sagebrush core area index (CAI), and c) sagebrush patch contiguity (CONTIG) with data from all four study areas.

[1] Partial dependence (measured by yhat or ŷ) measures the impact of one variable on the predicted outcome (here, probability of selection) of the response. A higher value corresponds to a higher probability of selection.

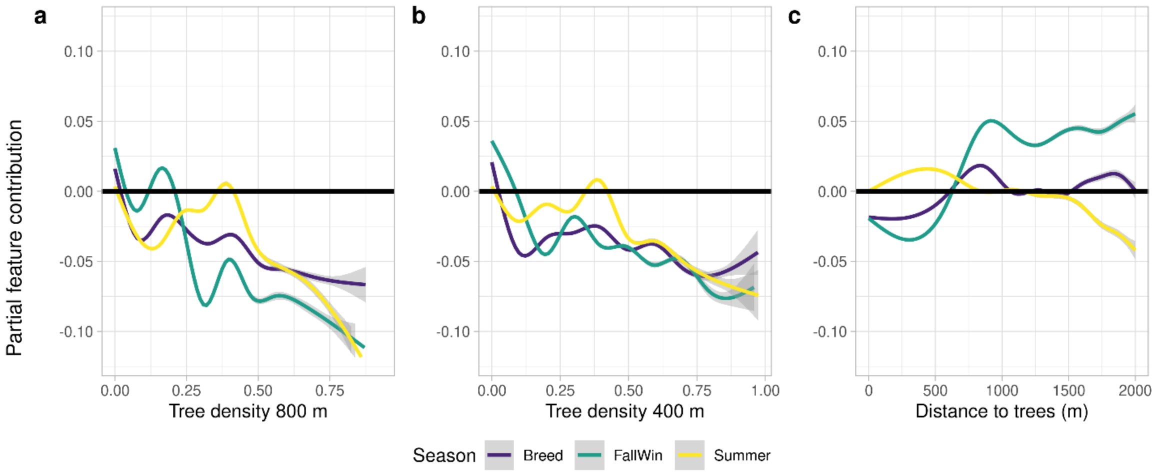

Figure 2.5. Feature contribution to model results in each season of a) density of treed pixels within 800 m (TREEDEN800), b) density of treed pixels within 400 m, and c) distance to trees (TREEDIST).

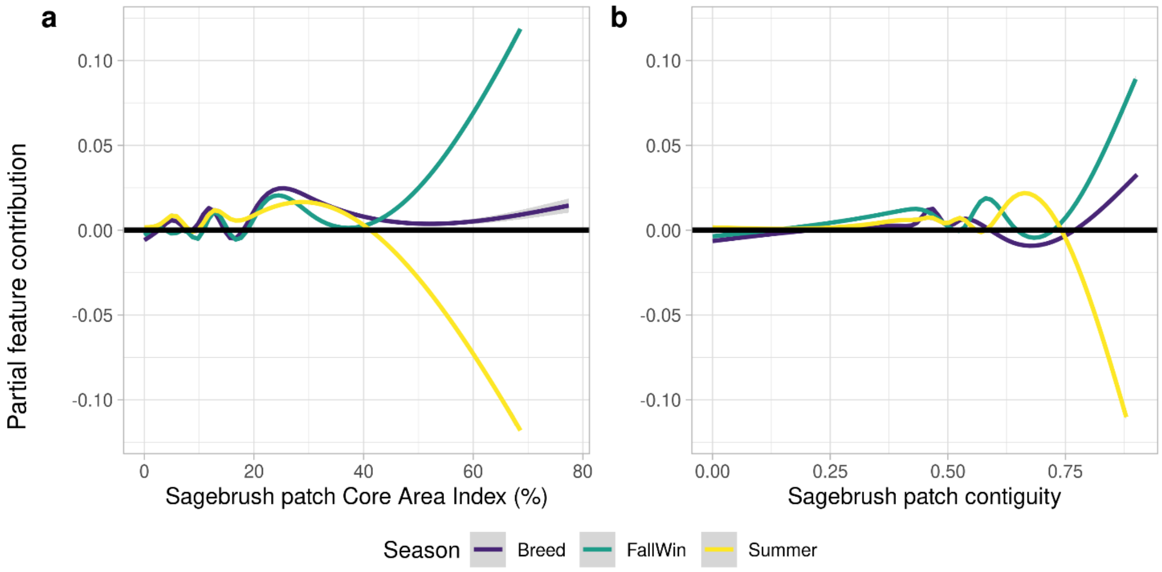

Figure 2.6. Feature contribution to model results in each season of a) sagebrush core area index (CAI) and b) sagebrush patch contiguity (CONTIG).

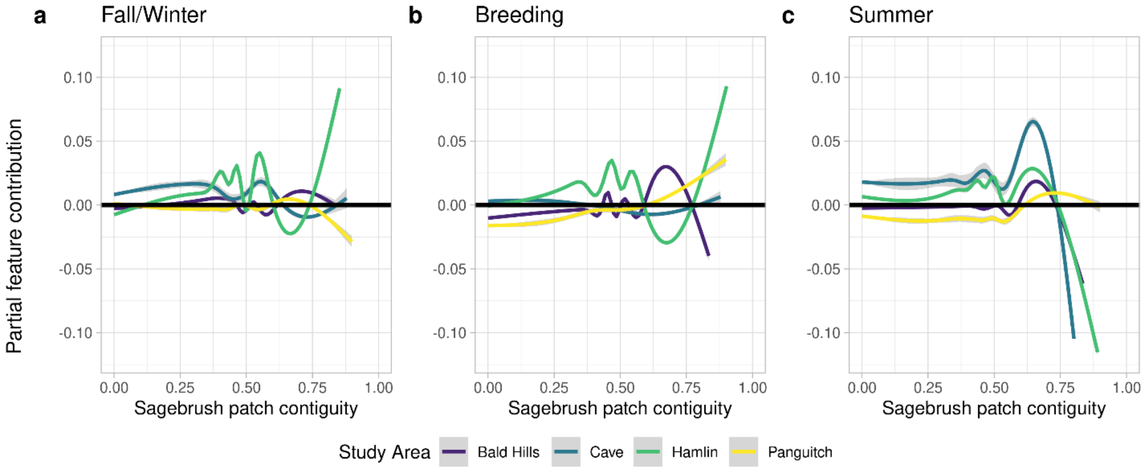

Figure 2.7. Feature contribution to model results in each study area and season of sagebrush patch contiguity (CONTIG).

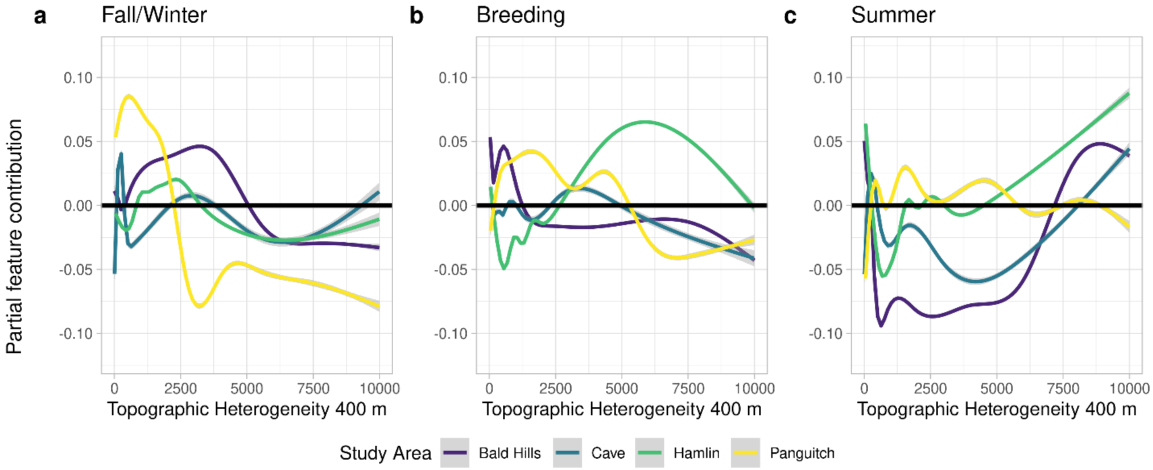

Figure 2.8. Feature contribution to model results in each study area and season of topographic heterogeneity index within 400 m (THI400).

CHAPTER III

GREATER SAGE-GROUSE FACE TRADEOFFS BETWEEN PREDATION RISK AND THERMAL EXPOSURE IN SELECTING HABITAT

ABSTRACT

Climate change is likely to drive widespread species range shifts and extirpations, the first of which will happen mostly on the warm edges of their range. That warm distribution edge tends to be fragmented, with lower quality habitat and lower population density and is more likely to experience threatening weather events. In the Intermountain West, climate will likely be warmer and drier in the future, driving a reduction in sagebrush (*Artemesia sp.*) and other shrubland cover. Among the species threatened by a hotter and more arid climate is the Greater sage-grouse (*Centrocercus urophasianus*), because they depend on sagebrush for forage and shelter. Other gallinaceous birds are sensitive to temperature extremes and exploit refugia to limit thermal stress. Sage-grouse likely do the same, but their response to temperature is not well studied. I deployed 75 data loggers across two valleys in southern Utah and Nevada and collected temperature and light intensity data every 30 minutes for 27 months. I used random forest models to test the impacts of temperature, land cover, and topography on sage-grouse habitat selection. I found that temperature influenced selection in all seasons and both sites. In Utah, the warmer site, sage-grouse used areas near trees during the winter and especially during summer, likely to avoid extreme cold and heat, respectively. In autumn and spring those extremes were less common and sage-grouse avoided habitat near trees. Conversely, sage-grouse in the cooler Nevada site were more likely to select large and contiguous patches of sagebrush in extremes periods but only selected habitat near trees

in winter cold, avoiding trees during summer heat. Sage-grouse also selected moderately heterogeneous terrain during thermal extremes. My 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 likely prefer to use sagebrush as thermal shelter but that it may be inadequate shelter during the hottest times, creating tradeoffs and forcing riskier selection. These models point towards a more mechanistic understanding of how sage-grouse distribution will likely retract at warm edges. This will refine our understanding of seasonal habitat requirements and inform management decisions of how to prioritize thermal refugia for an imperiled species of conservation concern.

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 in itself is not always the dominant driver of range limits (Arntzen and Espregueira Themudo 2008, Balzotti et al. 2016, Oldfather et al. 2020). In particular, 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). Further, 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 (*Artemesia 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 monophyla* 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 my 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, I 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. I 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.

METHODS

Study areas

I 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 3.1). 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 further 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 km^2), located further 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_{mean} = 19.8 °C) and the coldest was February (T_{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 km^2) 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. 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_{mean} = 19.6 °C) and the coldest was February (T_{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

I 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. I 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. I 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, I 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), I also included metrics of topographic position and heterogeneity. I 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

I 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. I 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, I 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, I positioned the logger 15 – 25 cm above the ground to mimic the conditions a sage-grouse would experience.

In July 2019 I 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, I was able to use data from 31 from Steptoe and 22 Buckskin. Of those deployed in 2019, I used data from 40 loggers from Steptoe and 28 loggers from Buckskin. For each logger, I 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 I 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, I 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, I created an interpolated surface at a 100 m resolution and aggregated the monthly averages by season. I 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 I did not include a separate measure of elevation in the habitat selection analysis to avoid problems of variable collinearity. I grouped September – November as Autumn, December – February as Winter, March – May as Spring, and June – August as Summer.

GPS data

For sage-grouse locations, I 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). I 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, I assessed their age, sex, mass, and body condition. I declined to put a transmitter on any grouse with an injury or a mass less than 1 kg. I 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.

The GPS transmitters logged four locations per day. For this study, I 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. I 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, I 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 I 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

I 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, I 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, I 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). I 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. I used 70% of the data for initial model training with a random subset of 30% of the data withheld for model validation. I 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, I 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, I 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 I 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, I 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. I repeated the process of dataset division ten times for each study area and season and report the average model performance metrics.

I 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. I 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 my 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 3.1). Buckskin had a higher mean temperature in summer months; Steptoe had a colder mean winter minimum temperature.

Model performance

I 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, I 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 3.2). Here, I 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 3.2). 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 3.2). 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 3.2).

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 3.2). 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 biggest 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. Further, 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 3.3). 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 my models suggest that extreme temperatures limit habitat selection. Partial dependence plots show that within each season, sage-grouse were most likely to select moderate temperatures and avoided extremes. In Buckskin, the probability of habitat selection dropped quickly and approached zero where temperatures in Summer exceeded roughly 35 °C, or 28 °C in Autumn (Figure 3.2). In Steptoe, the effect was similar but not as clear (Figure 3.3). Sage-grouse also selected moderate minimum temperature in Summer, Autumn, and Spring in both study areas. In Winter, the probability of selection decreased rapidly below a minimum temperature of -17 °C but then plateaued (Figure 3.4). Similarly, the partial dependence of selection on maximum temperature in Steptoe was not as limiting as in Buckskin—the rate of change of partial dependence was slower across the available temperature range in each season and the peak of selection was less distinct. These results indicate that sage-grouse selection varied across the available temperature range more in Buckskin than in Steptoe.

These results indicate the importance of temperature in sage-grouse habitat selection, but do not in themselves show how the birds respond to temperature. The two-way partial dependence plots I 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 3.5). Though sage-grouse rely on sagebrush, my results indicate that they did not select large or contiguous patches of sagebrush during high summer heat in Buckskin (Figure 3.6). 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 3.7). 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 3.8). 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 3.9). 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 3.11).

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 3.12a). 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 3.12b). 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 I recorded revealed differences in my 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. I did not measure precipitation, but measurements collected from temperature data loggers suggested that Buckskin was slightly warmer than Steptoe on average through 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 I did not build RF models of selection using PRISM data for comparison.

Further, 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 I 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

My results suggest that sage-grouse select habitat in response to temperature and that thermal extremes may be limiting. However, I 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 my 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 I 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, my 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). My 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 area 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 area 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 I 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. Further, the fact that sage-grouse in my 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. My 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 my models I did not use known temperature data at the exact location of each sage-grouse GPS detection. I also did not estimate temperature at each of those points based on interpolating temperature between the nearest data loggers. Instead, I 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 I detected. I 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

My 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 my 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, my data indicated that Utah's Buckskin Valley is marginally warmer than Nevada's Steptoe Valley. In combination with the fact that my 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 I 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. I 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.

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FIGURES AND TABLES

Table 3.1. Mean temperatures (°C) 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 3.2. 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	Mean Performance Difference
Steptoe	Autumn	Yes	0.6988	0.6825	0.8544	0.9516	0.7968	0.0636
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	0.0518
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	0.0539
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	0.0599
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	0.0143
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	0.0038
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	0.0250
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	0.0844
Buckskin	Summer	No	0.8269	0.8349	0.8215	0.9401	0.8559	

Table 3.3. 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
Steptoe	Autumn	Yes	T_{min}, T_{max}, T_{diff}, TREEDIST, CONTIG
Steptoe	Winter	Yes	T_{min}, T_{diff}, TREEDEN800, T_{max}, THI400
Steptoe	Spring	Yes	T_{max}, T_{diff}, TREEDIST, T_{min}, THI400, THI200
Steptoe	Summer	Yes	T_{min}, T_{diff}, TREEDIST, CONTIG, THI400
Steptoe	Autumn	No	TREEDIST, THI400, THI200, TREEDEN800, CONTIG
Steptoe	Winter	No	TREEDEN800, THI400, TREEDEN400, TREEDIST, THI200
Steptoe	Spring	No	TREEDIST, THI400, THI200, TPI400, TREEDEN800
Steptoe	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	Tmin, 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

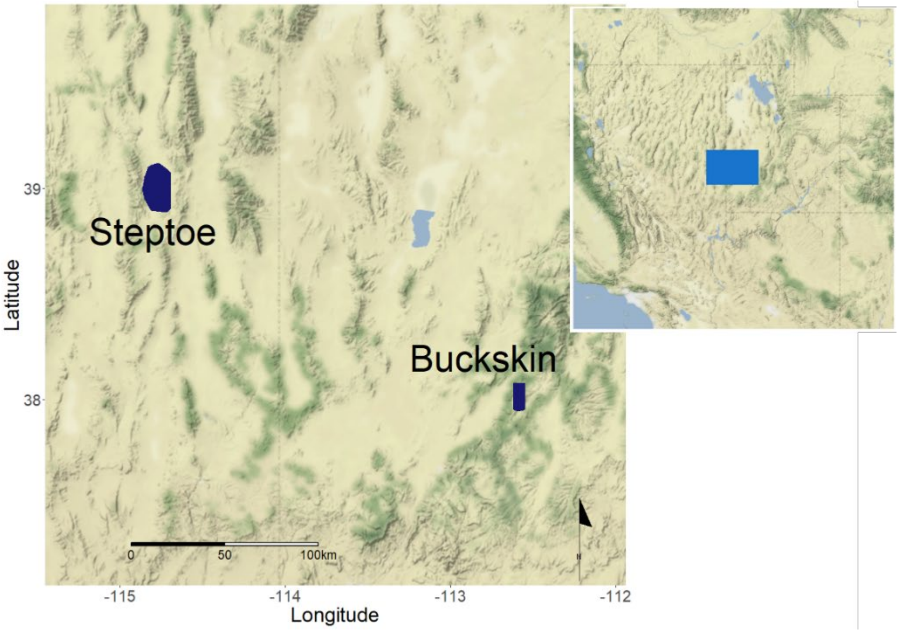

Figure 3.1. Study area locations in the western United States—Steptoe Valley, Nevada and Buckskin Valley, Utah—marked in dark blue with a minimum convex polygon around sage-grouse GPS data points collected there June 2019 – November 2020.

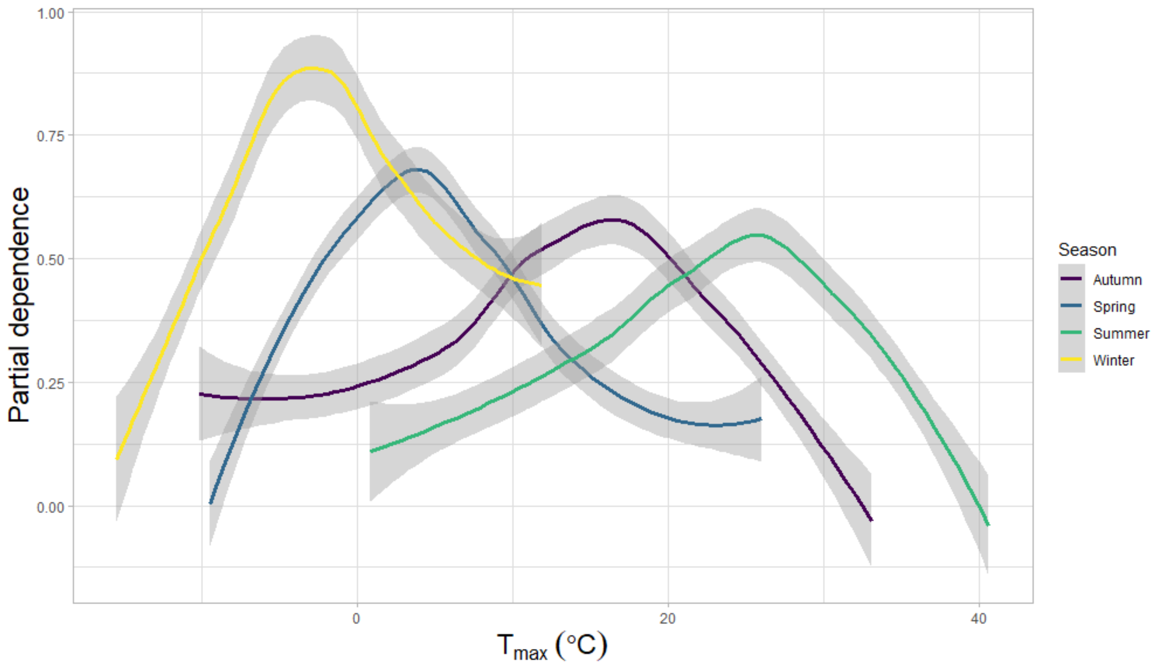

Figure 3.2. Marginal effect of average daily maximum temperature on sage-grouse habitat selection in Buckskin Valley, Utah across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

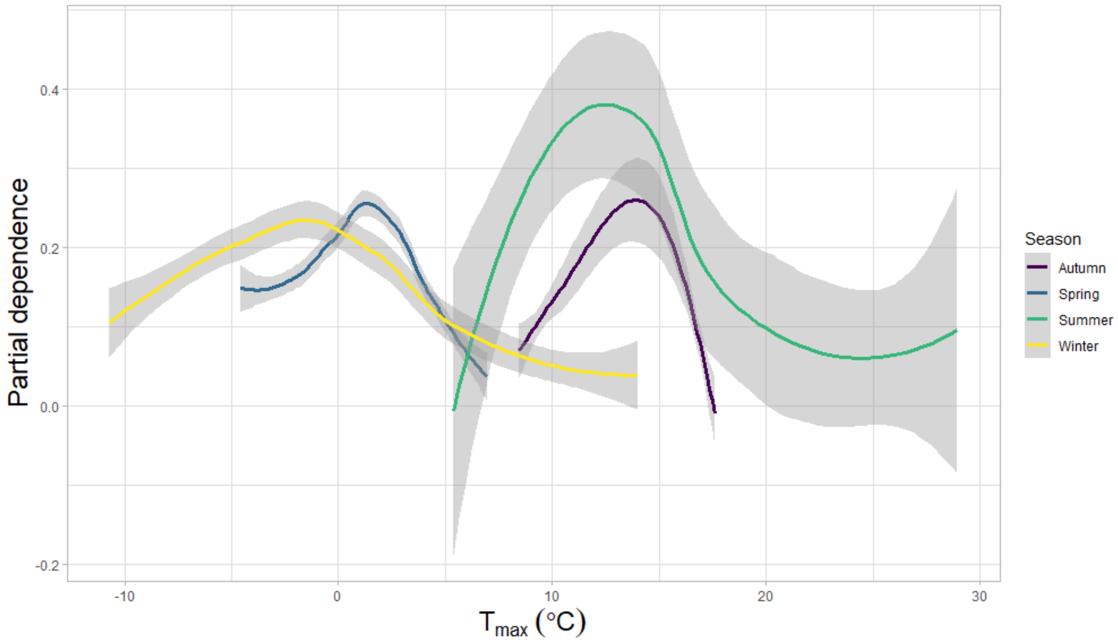

Figure 3.3. Marginal effect of average daily maximum temperature on sage-grouse habitat selection in Steptoe Valley, Nevada across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

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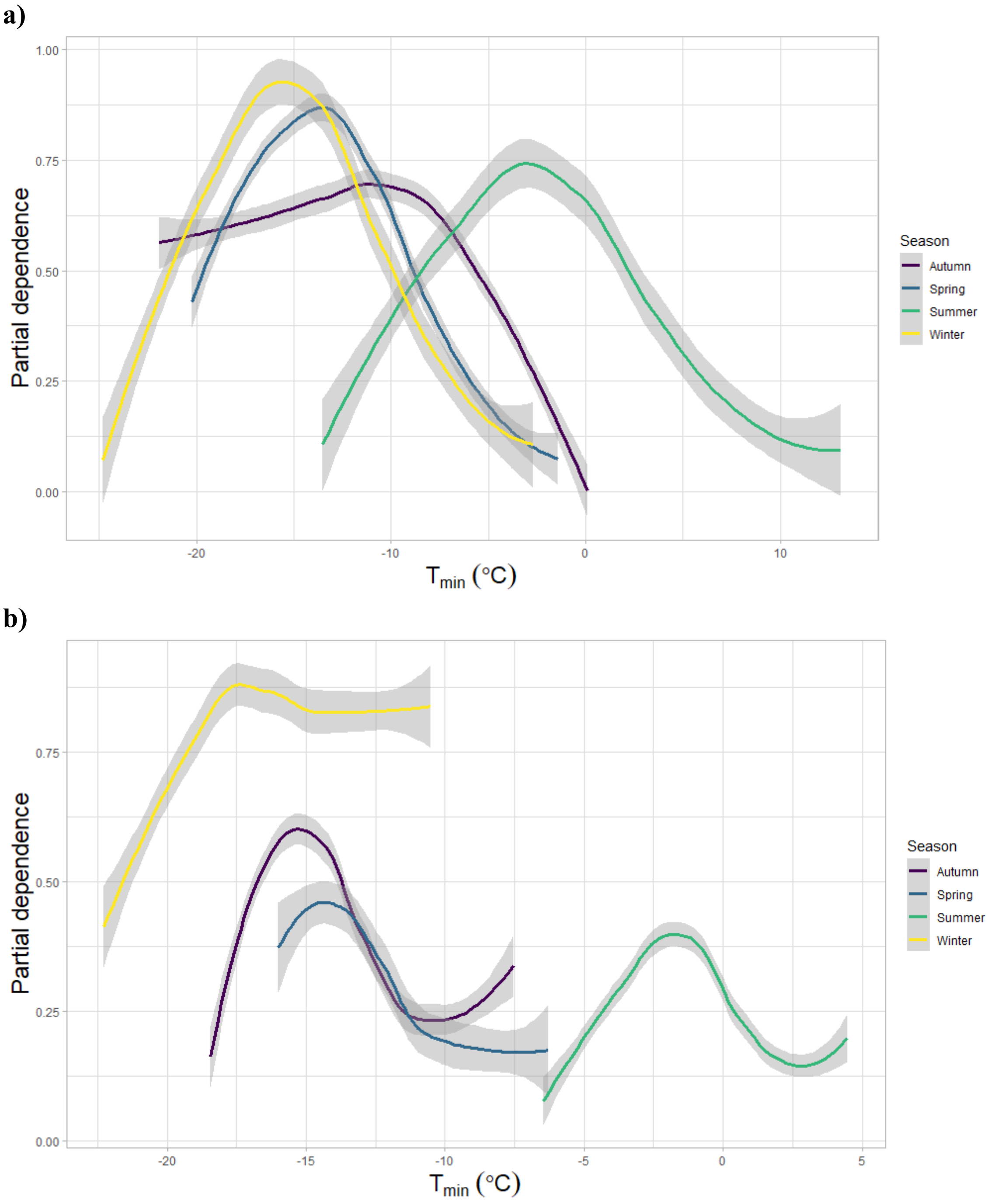


Figure 3.4. Marginal effect of average daily minimum temperature on sage-grouse habitat selection in **a)** Buckskin Valley, Utah and **b)** Steptoe Valley, Nevada across seasons, measured by partial dependence. Partial dependence measures the marginal effect of one covariate on the response variable when the effects all other covariates are held at their mean value. A higher partial dependence indicates a higher probability of selection.

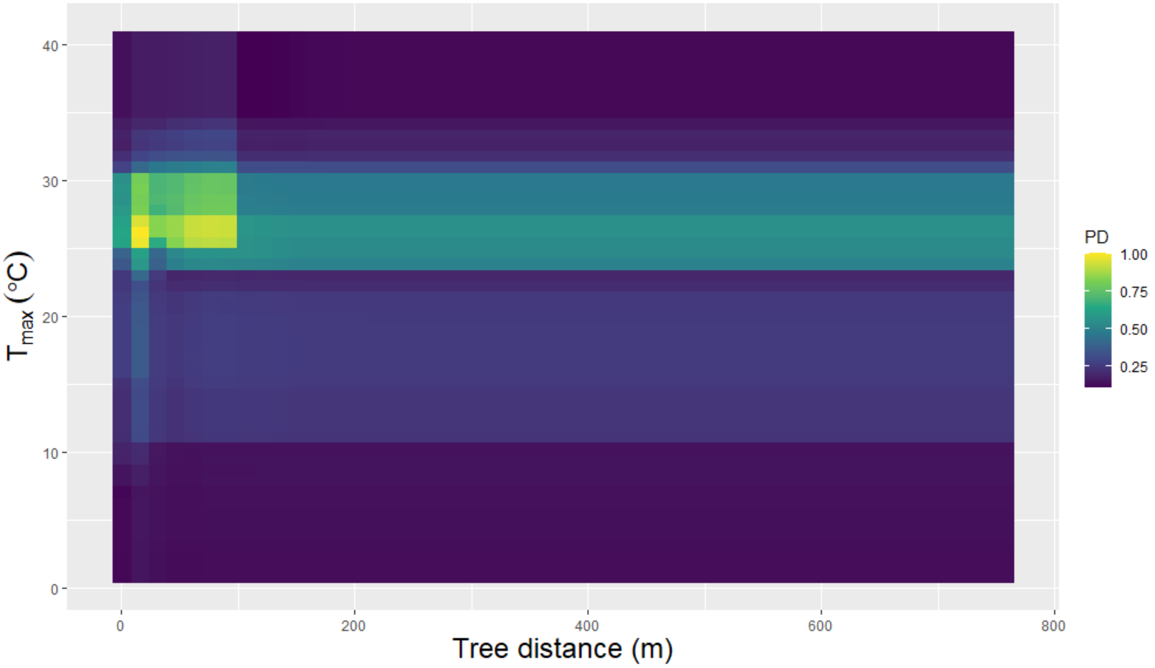


Figure 3.5. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to tree cover on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

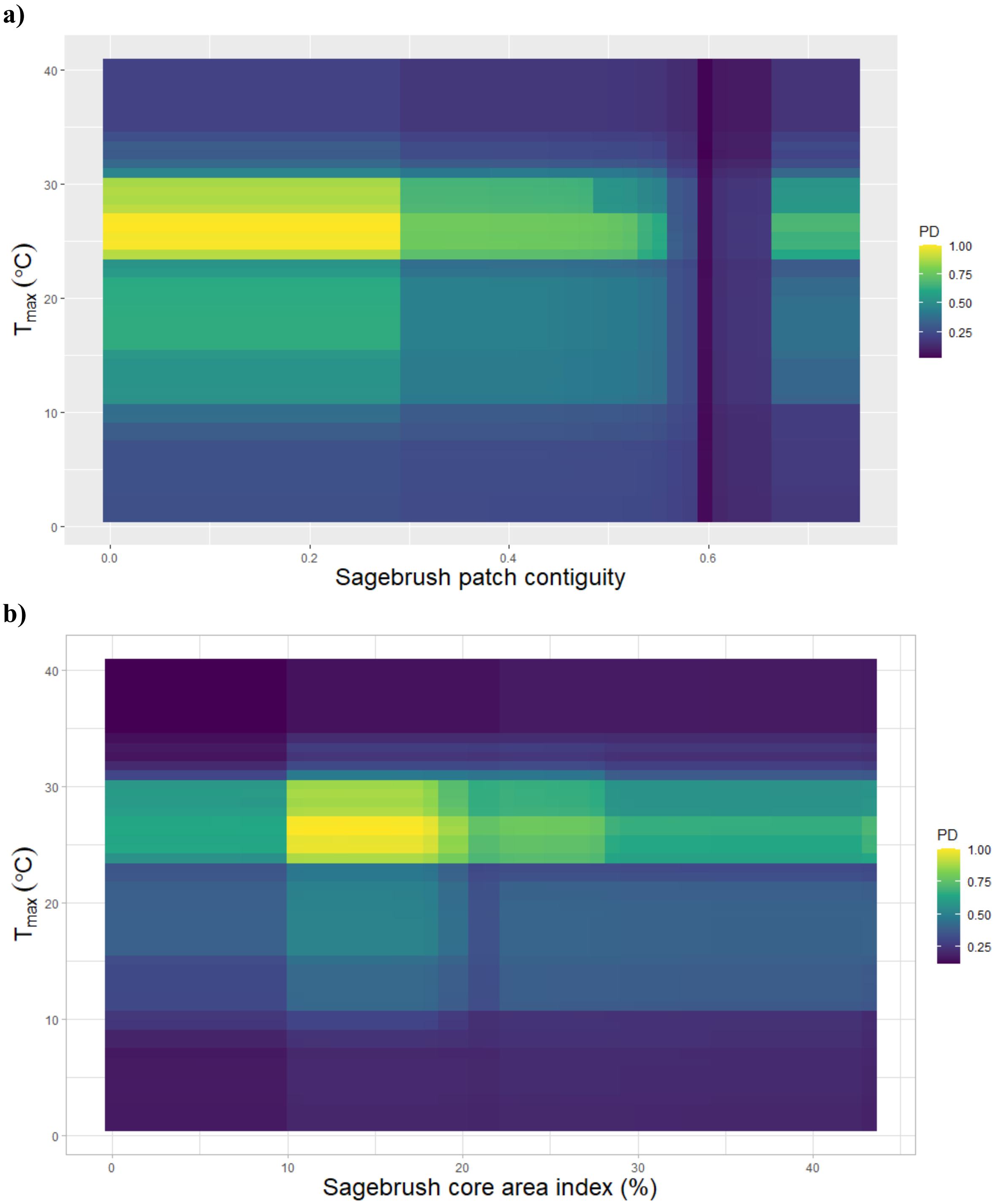


Figure 3.6. Marginal effects (partial dependence: PD) of average daily maximum temperature and **a)** sagebrush patch contiguity index (CONTIG) and **b)** sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

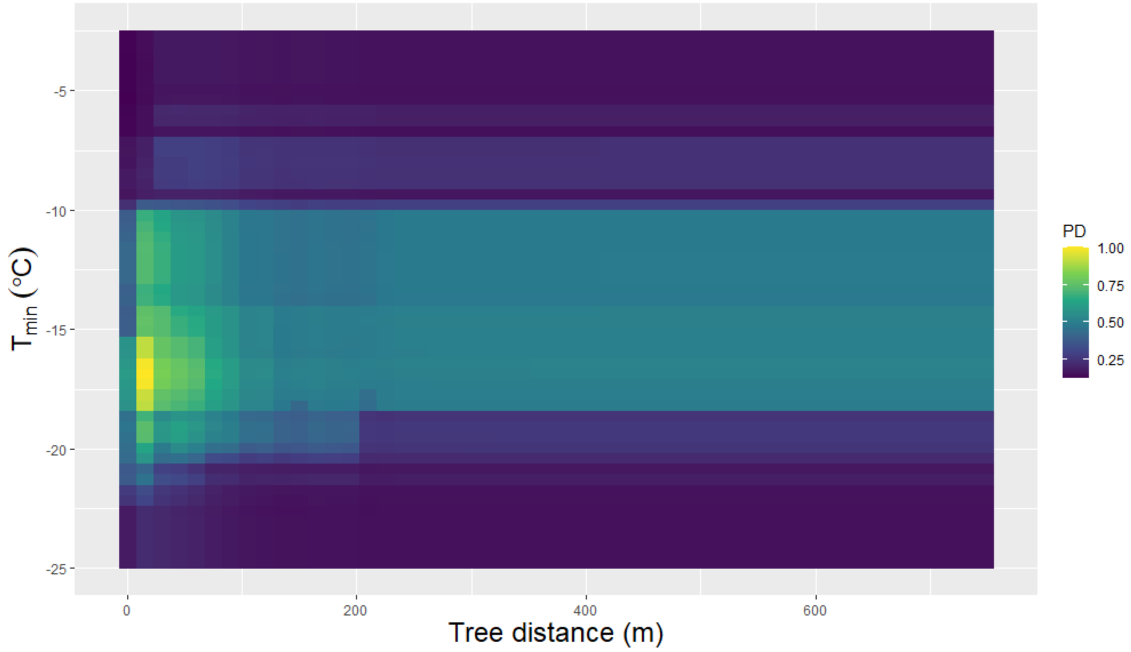


Figure 3.7. Marginal effects (partial dependence: PD) of average daily minimum temperature and distance to tree cover on sage-grouse habitat selection during winter in Buckskin Valley, Utah.

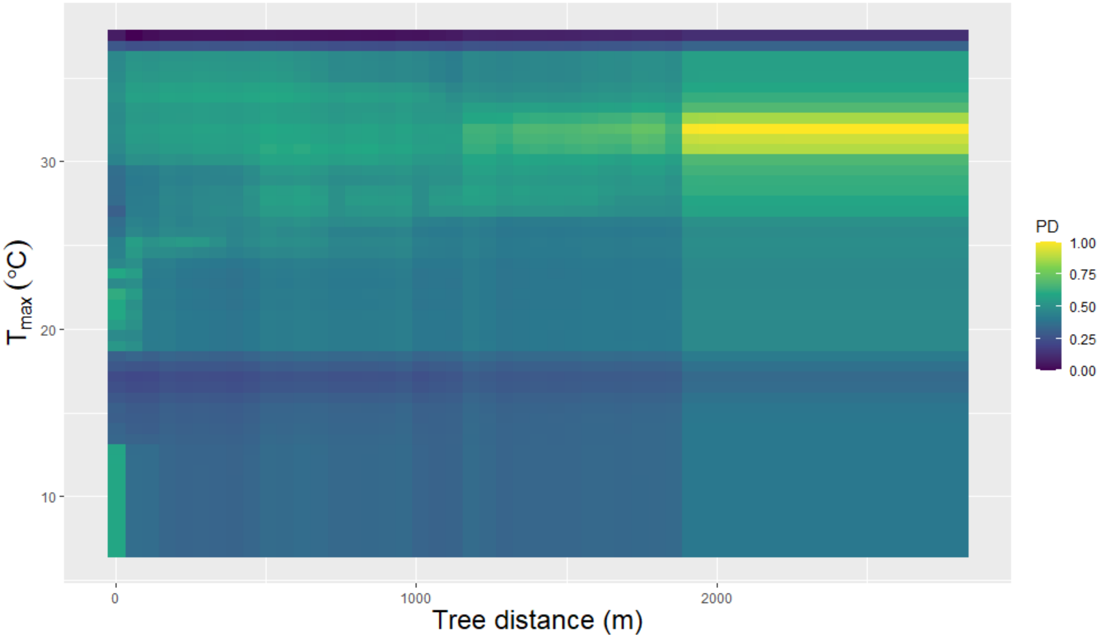


Figure 3.8. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to tree cover on sage-grouse habitat selection during summer in Steptoe Valley, Nevada.

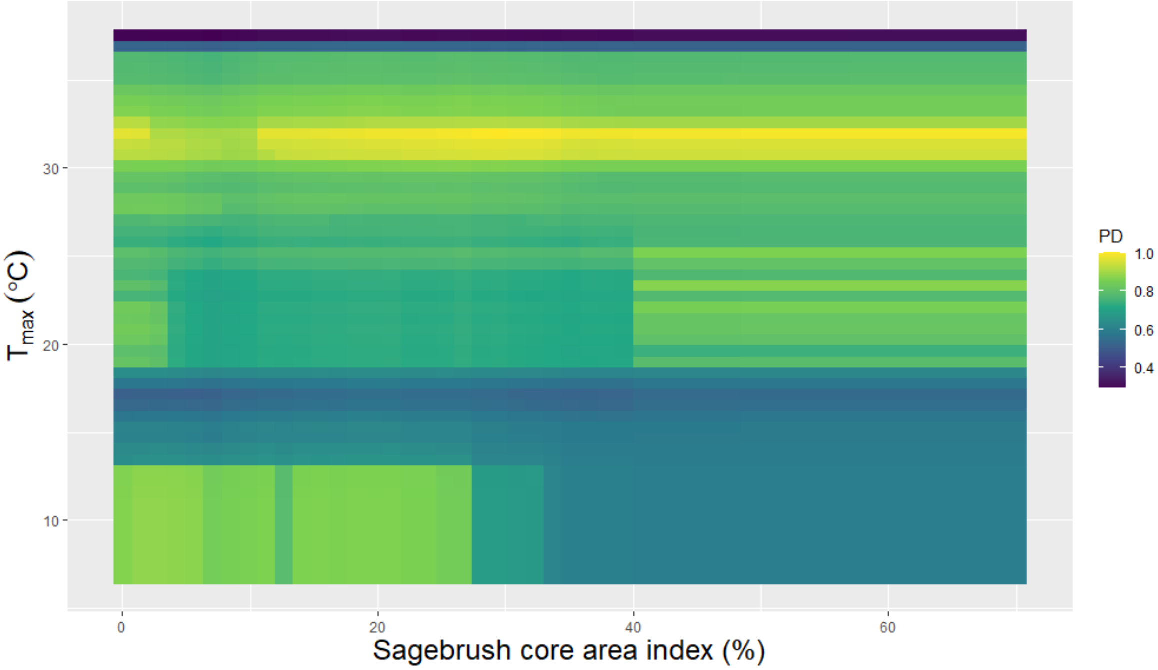
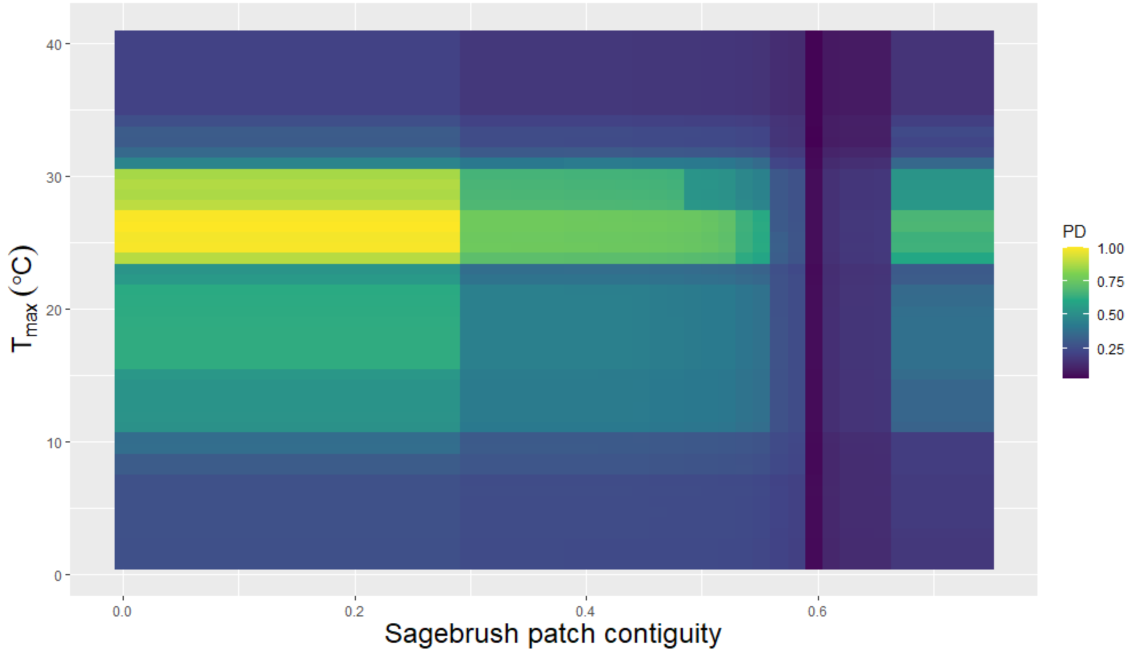


Figure 3.9. Marginal effects (partial dependence: PD) of average daily maximum temperature and sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Steptoe Valley, Nevada.

a)



b)

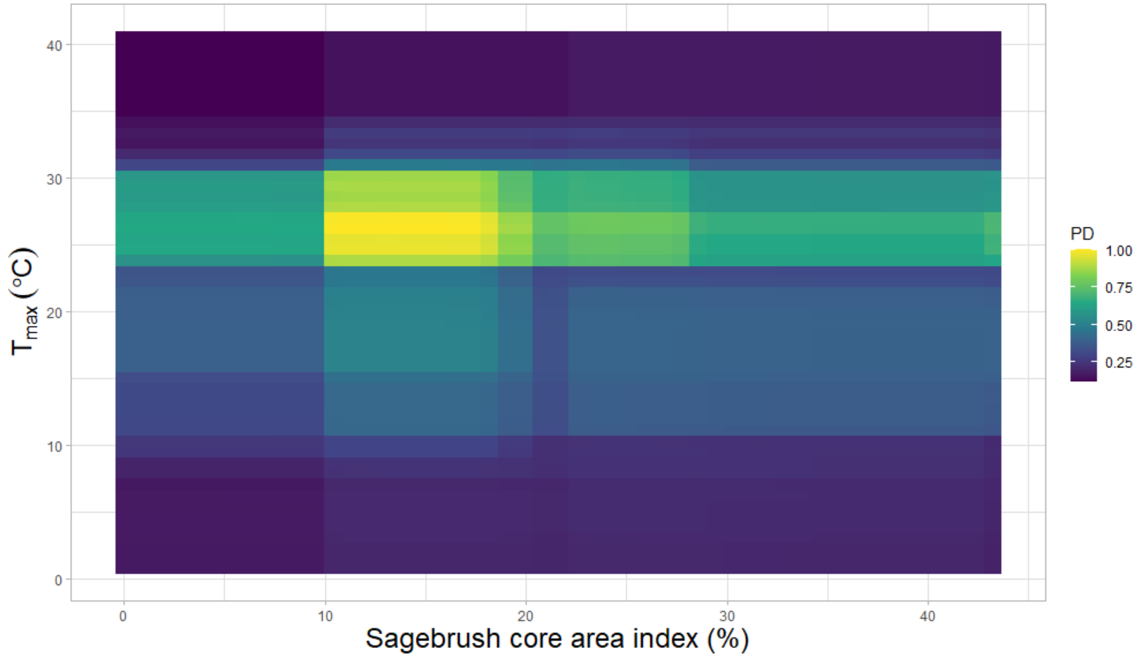
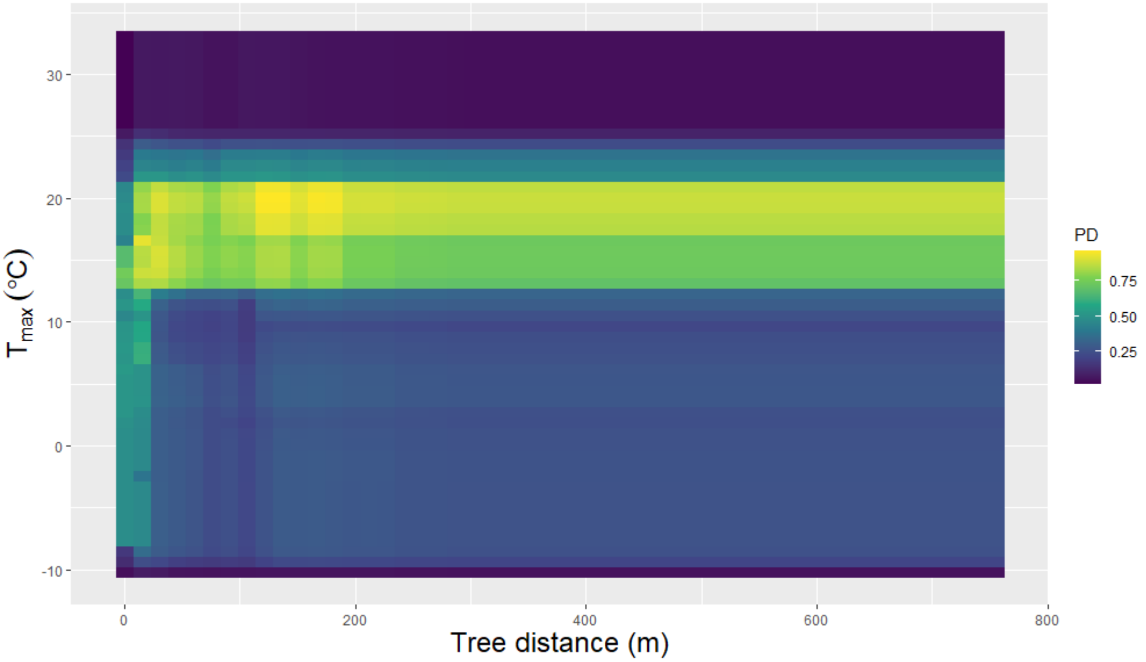


Figure 3.10. Marginal effects (partial dependence: PD) of average daily maximum temperature and **a)** sagebrush patch contiguity index (CONTIG) and **b)** sagebrush patch core area index (CAI) on sage-grouse habitat selection during summer in Buckskin Valley, Utah.

a)



b)

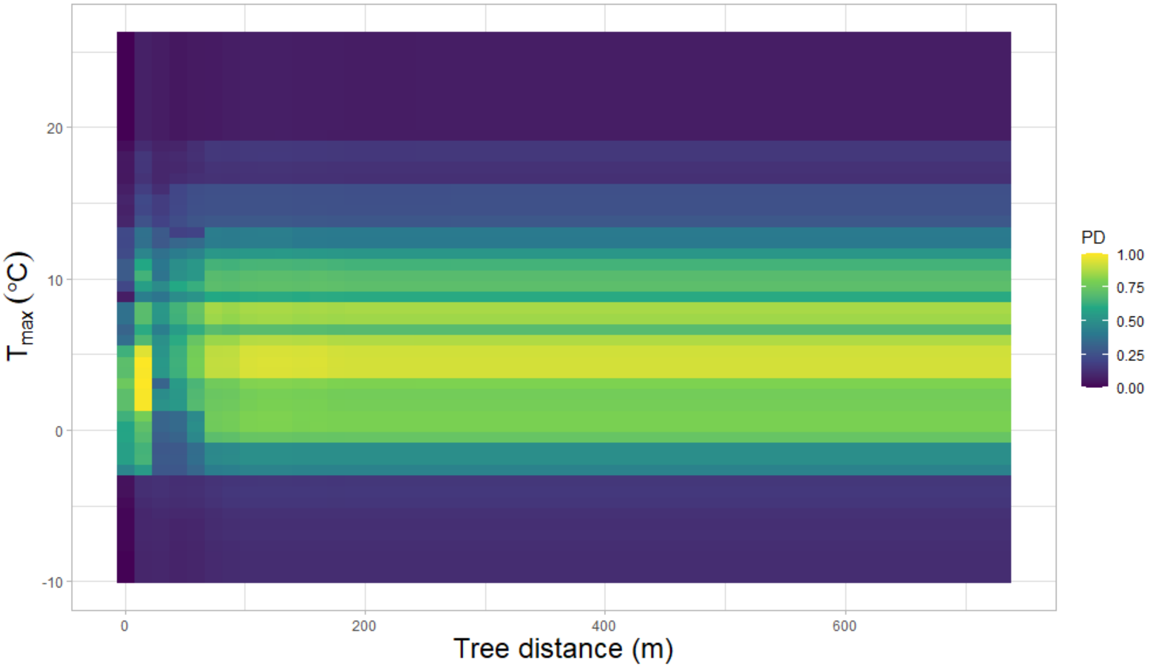


Figure 3.11. Marginal effects (partial dependence: PD) of average daily maximum temperature and distance to trees on sage-grouse habitat selection in Buckskin Valley, Utah during **a)** autumn and **b)** spring.

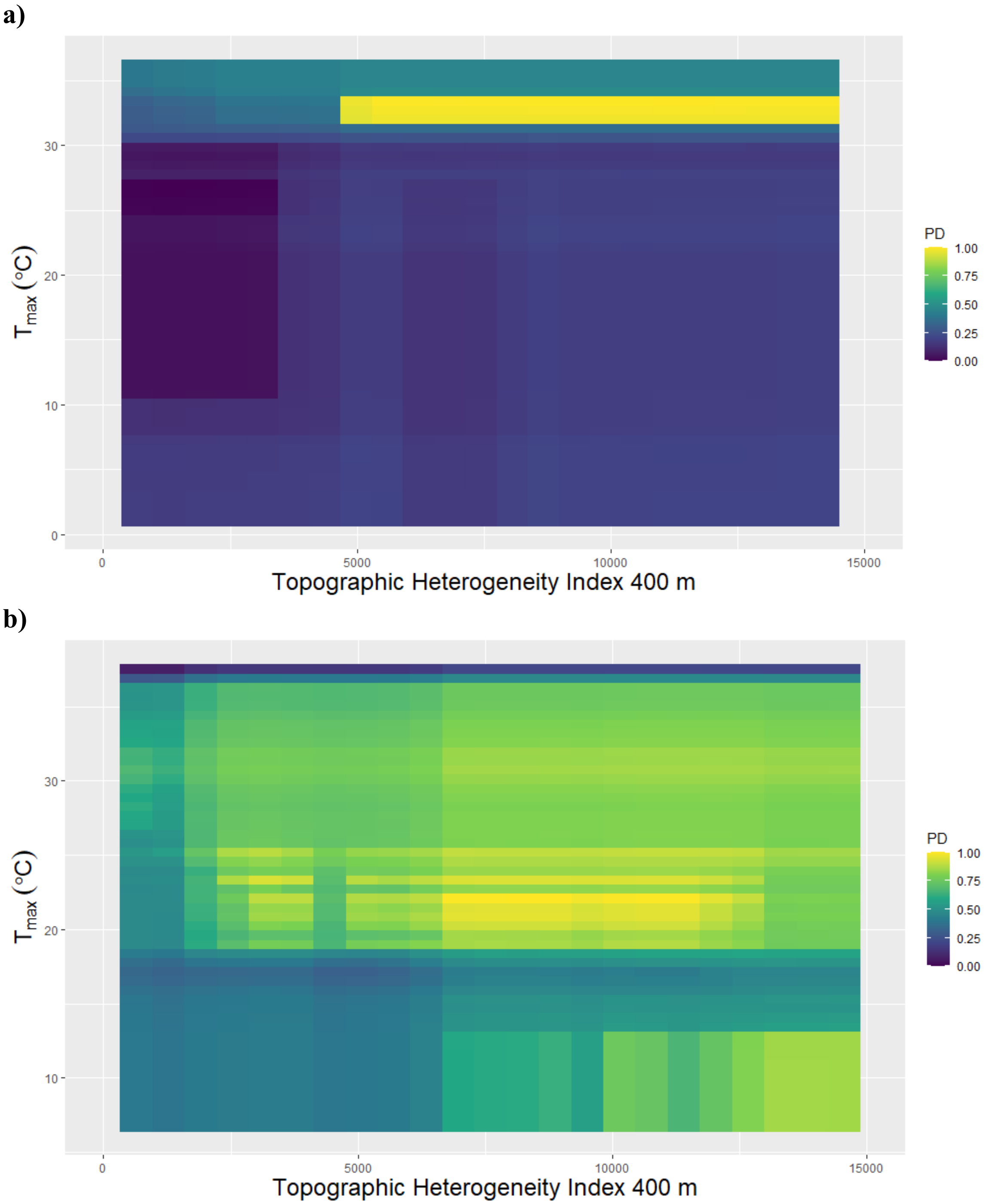


Figure 3.12. Marginal effects (partial dependence: PD) of average daily maximum temperature and topographic heterogeneity in a 400 m window on sage-grouse habitat selection during summer in **a)** Buckskin Valley, Utah and **b)** Steptoe Valley, Nevada.

CHAPTER IV

OPTIMIZED RANDOM FORESTS OUTPERFORM SIMPLE RESOURCE SELECTION FUNCTIONS AND REVEAL NOVEL HABITAT RELATIONSHIPS FOR GREATER SAGE-GROUSE

ABSTRACT

Wildlife habitat selection analysis (HSA) is an invaluable tool to understand wildlife-habitat associations, identify mechanisms driving distributions or population processes, and inform conservation and management. Resource selection functions (RSFs) have been the most common method of HSA for two decades. However, RSFs have limitations; they can be difficult to fit to nonlinear relationships and assume independence of samples and no collinearity between covariates. This suggests utility in exploring other methods for HSA. Among the methods that have been more recently used is random forest (RF), a nonparametric method that is able to model nonlinear relationships and interactions and does not assume independence of samples. Here, I optimized RF for HSA and compared its findings and performance in predicting out-of-sample data with those of RSFs using >116,000 GPS locations for greater sage-grouse (*Centrocercus urophasianus*) in four study areas in southern Utah and Nevada. I found that RF outperformed RSF in predicting both withheld data from within the study area used for model training and data from each other study area. I also found that RF detected nonlinear relationships that were obscured in the RSFs. My findings suggest that when used appropriately, RF is a valuable tool to better inform wildlife conservation and management decisions and RF should be considered when selecting methods for HSA,

especially when nonlinear relationships are hypothesized, interactions are likely, and there is a large chance for autocorrelation between samples.

INTRODUCTION

The processes defining wildlife habitat requirements function at multiple scales (Wiens 1989, DeCesare et al. 2012, Vale et al. 2014, McGarigal et al. 2016). While species distribution models (SDMs) are useful tools to understand large-scale associations, wildlife habitat selection research is essential to more precisely understand the factors driving species distributions. Currently, the most common way to model wildlife habitat selection is to use resource selection functions (RSFs), an implementation of conditional or mixed effects generalized liner models, to compare the characteristics of habitat used by animals to that available to them (Manly et al. 2002, Johnson et al. 2006, Lele et al. 2013, McDonald 2013, Northrup et al. 2013). These are effective and versatile models; however, like any analysis tool, they have limitations. In particular, the simplest form of RSFs assume independence of samples and no collinearity between independent variables and are more difficult to fit if a nonlinear relationship exists, all of which may make them imperfect for analyzing habitat selection and species distributions. There has been considerable work to address those potential issues, including methods to allow researchers to better account for nonlinear effects and interactions, including by using higher-order polynomials, generalized additive models (GAMs), or multivariate adaptive regression splines (MARS) (Elith et al. 2006a, Aarts et al. 2013, Michelot et al. 2019, Avgar and Betini 2020, Lazenby et al. 2021, Northrup et al. 2022), that have been invaluable in advancing analyses of animal habitat selection. However, many of those methods require more advanced technical expertise to implement than the simple RSF accessible to most practitioners and there is no clear consensus on the best way to manage RSF shortcomings. Therefore, it is likely important to evaluate other means to study habitat selection and continue to add to the toolbox of potential analytical methods.

Among the many methods for analyzing wildlife-habitat relationships are several machine learning algorithms such as random forests (RF), artificial neural networks (ANN), support vector machines (SVM), and gradient boosting methods. These are relatively new to ecology and have been critiqued for reduced interpretability, but have been gaining recognition as powerful and efficient tools for many areas of ecological research (Elith et al. 2006a, Cutler et al. 2007, Olden et al. 2008, McDonald et al. 2013, Stupariu et al. 2021), and there have been many efforts to “demystify” machine learning for applications in ecology in both their use and interpretation (Thuiller et al. 2003, Elith et al. 2006a, Leathwick et al. 2006, Olden et al. 2008). Machine learning techniques tend to be well-equipped to handle large, chaotic datasets with the nonlinear effects and interactions abundant in ecology (Recknagel 2001, Cutler et al. 2007, Cushman and Huettmann 2010, Kampichler et al. 2010, Cushman and Wasserman 2018). Also, many have advantages over traditional statistical methods, as they do not have the same assumptions of these traditional methods that ecologists are sometimes forced to violate (Recknagel 2001, Cutler et al. 2007, Kampichler et al. 2010).

Compared to a simple RSF, some machine learning methods allow greater flexibility while not precluding rigorous hypothesis testing. RF is one such relatively intuitive machine learning model that is gaining attention in ecological studies. RF is a nonparametric, tree-based ensemble learning method that builds on decision trees to improve on the performance of individual trees (Breiman 2001) and there are many available methods to interpret the results and use the models to explain ecological phenomena (Ryo et al. 2020). RF has been used effectively to analyze animal habitat selection and species distributions and performs well in predicting new data (Kampichler et al. 2010); furthermore, in previous work RF has outperformed conventional methods like RSF in both descriptive and predictive capacity (Evans and Cushman 2009, Carrasco et al. 2014, Doherty et al. 2016, Severson et al. 2017b, Shoemaker et al. 2018, Reisinger et al. 2021a, Shanley et al. 2021).

RF is especially useful in ecology when we anticipate nonlinear effects and interactions between covariates (Cutler et al. 2007). Because RF makes no assumptions about data distribution, error structure, or independence of samples, it does not impose *a priori* model selection can effectively describe variability in environmental covariate impacts without sacrificing predictive capacity when tuned appropriately. RF may also be suited to these sorts of analyses because of the fundamentally nonlinear nature of niches in covariate space (Cushman et al. 2010). Therefore, RF is also a particularly valuable tool in systems where there is little wildlife location data (Mi et al. 2017), where habitat selection is expected to vary over the extent of the study (Doherty et al. 2016), and when fragmentation or range edges make heterogeneous effects likely (Baruch-Mordo et al. 2013, Cushman et al. 2017).

Study system

Greater sage-grouse (*Centrocercus urophasianus*, hereafter “sage-grouse”) are sagebrush (*Artemisia sp.*) obligates threatened by habitat loss and fragmentation (Braun 1998, Connelly et al. 2000). In evaluating sage-grouse habitat associations, many different methods have been successfully used to identify the most important environmental conditions at various scales (Sandford et al. 2017, Picardi et al. 2020, 2021). At regional and range-wide scales, there are clearly established habitat needs for population persistence: large, unbroken tracts of sagebrush with minimal fragmentation by human land use (e.g., agriculture), forest, desert, grassland, or overly rugged topography (Aldridge et al. 2008, Knick et al. 2013). However, there is considerable variety in the microhabitat selected by individuals across sage-grouse distribution, which suggests variability in both the limiting environmental factors and the selection for available habitat and food resources. This underscores the need to make management and conservation decisions based on range-wide, regional, and local environmental conditions (Doherty et al. 2010b, 2016, Fedy et al. 2014, Smith and Olsen 2020). It is clear that sage-grouse habitat selection varies regionally (Doherty et al. 2016, Dahlgren et al. 2019, Picardi et al. 2020), so it is critical to assess the factors driving habitat selection and suitability in different areas, and especially along range margins (Vale et al. 2014). Along their southern range margin, sage-grouse are exposed to particularly fragmented and low-quality habitat (Miller and Eddleman 2001). Differences in selection across sage-grouse distribution are critical to identify, as they will tie directly to different habitat limitations for disparate populations and varying probabilities of extirpation (Aldridge et al. 2008, Coates et al. 2021).

Though sage-grouse are sagebrush obligates, they also require other vegetation types seasonally, and there is likely a nonlinear impact of sagebrush cover on habitat quality (Drut et al. 1994, Connelly et al. 2000, Dahlgren et al. 2019). There are also likely thresholds in sage-grouse response to tree cover (Baruch-Mordo et al. 2013, Prochazka et al. 2017, Severson et al. 2017b) and temperature (Beers and Frey 2022b). The level of fragmentation and the extreme range of temperatures existing in the sagebrush communities of the southern Great Basin suggest that RF might be an appropriate technique to analyze sage-grouse habitat selection there.

The purpose of this study was to determine if RF is an appropriate tool for modeling greater sage-grouse habitat selection along the patchy, fragmented southern edge of its distribution, using a conventional RSF for comparison. For this comparison of HSAs, I evaluated the factors of land cover and topography that impact sage-grouse habitat selection. In particular, I examined the ways in which topography and sagebrush patch characteristics influence selection in the presence of trees. I hypothesized that RF would detect nonlinear effects missed by the simple RSFs, especially thresholds beyond which selection would change markedly. I also hypothesized that RF would outperform RSF in predicting out-of-sample data. The ability to more precisely describe factors driving sage-grouse habitat selection at local scales will be critical for developing the most effective conservation efforts (Smith and Olsen 2020). By testing the strength of RF models in this system, I aim to provide a means to leverage sage-grouse location data for better place-based conservation and management and contribute to ongoing work expanding the toolbox for HSAs.

METHODS

Study region

My study region included four distinct study areas (Figure 4.1) along the sage-grouse southern range margin in the southern Great Basin of Nevada and Utah, described as Great Basin-Colorado Plateau sagebrush semi-desert; this region is more xeric than sage-grouse habitat in most of their distribution (West 1983b, Miller and Eddleman 2001). I worked in four study areas, each one a valley bounded by mountains, characteristic of the Basin and Range province. In Utah, the sites were in the Bald Hills, Hamlin Valley, and Panguitch sage-grouse management areas (SGMAs; Utah Public Lands Policy Coordination Office 2019). In Nevada, the study areas were in northern Hamlin Valley in the Lincoln population management unit (PMU) and in the Cave/Steptoe PMU (Emm et al. 2019). The elevation in each study area ranged from 1500 – 2600 m in the Bald Hills, 1800 – 2800 m in Cave, 1800 – 2700 m in Hamlin, and 2000 – 2800 m in Panguitch.

Sagebrush in this region can be dominant in some areas (>90% of land cover), especially in the lowest elevation, which are often xeric areas where *A. nova* and *A. arbuscula* were most common. Elsewhere, *A. tridentata wyomingensis* and *A. tridentata vaseyana* were most common. Where land cover is not dominated by sagebrush, common plant cover includes rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.), horsebrush (*Tetradymia* spp.), bitterbrush (*Purshia tridentata*), Mormon tea (*Ephedra* spp.), winterfat (*Krascheninnikovia lanata*), native bunchgrasses, cheatgrass (*Bromus tectorum*), and a variety of grasses and forbs. In this region, sage-grouse habitats are threatened by mixed forests of pinyon pine (*Pinus edulis* and *P. monophyla*) and juniper (*Juniperus sp.*) encroaching into historic sagebrush communities, which both fragments the sagebrush cover and increases the risk of depredation by avian predators (Doherty et al. 2010b, Baruch-Mordo et al. 2013, Coates et al. 2017, Severson et al. 2017a, 2017b). In high elevation areas of the study region, woodlands were the most common cover, including quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus sp.*), juniper, pinyon pine, spruce (*Picea sp.*), and fir (*Abies sp.*). Many high elevation areas also include patches of sagebrush.

Environmental data

In this study, I used metrics of topography and land cover to evaluate my hypotheses. I downloaded land cover data from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE; Rollins 2009) and derived from those data five metrics of the land cover most important to sage-grouse. Because sagebrush patch size and configuration can influence sage-grouse persistence or extirpation (Wisdom et al. 2011), I calculated metrics of sagebrush patch contiguity (CONTIG) and core area index (CAI) using the R package *landscapemetrics* (Hesselbarth et al. 2019). It is well established that tree cover negatively impacts sage-grouse lek occupancy and habitat selection (Aldridge et al. 2008, Baruch-Mordo et al. 2013, Prochazka et al. 2017, Coates et al. 2021), but there is some evidence for sage-grouse exhibiting maladaptive or high risk selection and for potential thresholds and interactions between environmental variables in sage-grouse response to trees (Coates et al. 2017, Cutting et al. 2019, Pratt and Beck 2021, Beers and Frey 2022a). I therefore calculated the distance to any pixel of a tree or woodland cover type (TREEDIST). I also calculated the density of those pixels within 400 m (TREEDEN400) and 800 m (TREEDEN800) moving windows for metrics of overall tree cover nearby.

Evidence for sage-grouse response to terrain is mixed. Most evidence suggests that flatter terrain is associated with greater sage-grouse survival, lek persistence, and habitat selection, but some evidence points to a potential role of topographic heterogeneity in providing cover from avian predators (Dinkins et al. 2014, Beers and

Frey 2022a). I built topographic metrics using a digital elevation model (DEM) of 10 m resolution using the R package *elevatr*. To capture potential impacts of terrain, I included metrics of both topographic position and heterogeneity. Topographic Position Index (TPI: Jenness et al. 2013) measures the degree to which a pixel in a DEM is higher or lower than the pixels around it within a user-defined distance. A low value indicates a pixel is lower than those around it (e.g., a valley, sink, ravine), a high value corresponds to a geographic high point (e.g., a peak or ridge), and a value of zero describes flat ground or where a pixel is equally higher and lower than the pixel around it (e.g., on a slope that is uniform within the user-defined window). Topographic Heterogeneity Index (THI) measures the overall ruggedness of terrain in an area by calculating the sum of the absolute value of every pixel's TPI value within the same user-defined window size. In this study, I used window sizes of 50 m, 200 m, and 400 m.

Used and available data

I used GPS telemetry data collected 2014-2020 from sage-grouse fitted with rump-mounted, solar-powered GPS transmitters (Geotrak, Inc., Apex, NC; Microwave Telemetry Inc., Columbia, MD). These data came from capture efforts similar to Giesen et al. (1982). After being captured, grouse were weighed, sexed, aged, and checked for injury. The GPS transmitters were programmed to collect four points each day: dawn, midday, dusk, and night. After removing data points that were clear outliers, from within the first 48 hours of handling, and from individuals with fewer than 100 successful fixes, the dataset included 116,310 points from 96 sage-grouse (median n = 1398 locations/sage-grouse).

Because I analyzed habitat selection by individual sage-grouse, I treated this study as 3rd order habitat selection (Johnson 1980). For each individual, I estimated 90% home ranges using a kernel density estimator with the default settings from the R package *adehabitatHR* (Calenge 2017). Within each home range, I sampled the available environment at a ratio of ten available points for every used point, which created a dataset of more than 1,339,000 availability data points.

Sage-grouse habitat requirements vary seasonally (Connelly et al. 2000, Dahlgren et al. 2016); therefore, I split the dataset into three seasons relevant to sage-grouse: Breeding (March – May), Summer (June – September), and Fall/Winter (October – February). Then I fit models for each combination of study area and season and for both the entire study region and each study area across all seasons, yielding a total of 16 model conditions.

Resource selection functions

I analyzed sage-grouse habitat selection by two different methods. The first is the most common in animal habitat selection studies: a mixed effects generalized linear regression, in this context called a resource selection function (RSF) (Boyce et al. 2002, Gillies et al. 2006, Johnson et al. 2006). This is the most straightforward means to implement an RSF; though there are many techniques to explicitly account for nonlinearities and interactions, they tend to require more statistical skill and *a priori* assumptions. First, I standardized covariates by their standard deviation for use in the RSF models. I used individual sage-grouse ID as a random effect with a random intercept, fitted using the R package *lme4* (Bates et al. 2012). I selected the best fit models in an information theoretic framework using Akaike's information criterion corrected for small sample size (AICc) (Burnham et al. 2011). I excluded from consideration any models with excessive correlation between predictor variables (|r| > 0.5) and dropped variables with a variance inflation factor greater than 10 (Naimi et al. 2014). For each model I calculated the most important variable using the R package *relaimpo* (Gröemping and Lehrkamp 2021).

Random forests

Though RF and other machine learning methods have been used with increasing frequency to analyze animal distributions and habitat selection and have outperformed conventional RSFs in the past, there is no apparent consensus about standard means of data preparation, model training, and model evaluation. Some have described best practices (e.g., Roberts et al. 2017, Cushman and Wasserman 2018, Zhang et al. 2019, Valavi et al. 2021), yet there are still many ways in which ongoing research efforts differ, and ways to improve habitat selection models using RF should be explored.

This is not the first study to compare RF and RSF for habitat selection. Shoemaker et al. (2018) found that RF outperformed RSF in cross-validation and detected ecological effects not found by RSF. I chose RF in this study to further explore the best practices for using novel methods for habitat selection analyses and build on existing work. I also chose RF because it is among the machine learning methods that has performed well in ecological analyses, is intuitive to implement, and is easily interpreted. Because RF is fairly intuitive and easy to use, it is important to account for potential shortcomings that are not immediately obvious—implementing RF for used-available data carries some risks of overfitting, inaccurately sampling the environment, and improperly assessing model performance (Roberts et al. 2017). In this study I implemented RF models to account for the hierarchical nature of habitat selection data and properly sample the available environment while maintaining a simple implementation to best evaluate RF's utility as a HSA tool.

Class imbalance

One ongoing point of disagreement is the problem of class imbalance, especially for RF models, which tend to underperform with a large imbalance between classes of the response variable (Evans and Cushman 2009, Shabani et al. 2016). Habitat selection analyses begin as presence-only data and remains analogous in their methods (McDonald 2013, McDonald et al. 2013). Because there is no natural ratio in used-available data, there are competing considerations for its design, including issues due to oversampling from one class of the response (Chen et al. 2004, MacKenzie 2005, Boyce 2006, Valavi et al. 2021).

The function of the "available" data is to provide a meaningful representation of the environment animals could have chosen to compare against the locations they did select, which suggests sampling many times the number of "used" data points (Franklin 2009, Renner et al. 2015). However, sampling large numbers of available points naturally creates considerable class imbalance and overlap in the environmental conditions of the used and available data, which can lead to poorer performance in developing rules to distinguish the two classes and to overfitting when deep trees are fit (Ali et al. 2013, Valavi et al. 2021). RF models are grown to minimize the error in predicting out-of-bag (OOB) data during model training. Yet with severe class imbalance, OOB error is minimized by focusing on accurately predicting mostly the majority class. This can yield poor results for habitat selection data, as the final model will be trained to reduce the error predicting available habitat without describing the used habitat and the models are more likely to miss important ecological phenomena by chance (Ali et al. 2013). Further, oversampling may not accurately represent the choices wildlife face, as nearby pixels of high resolution likely do not represent meaningfully distinct selection options.

One solution with imbalanced data is to induce a balanced dataset used in the RF, either by equal sampling (Barbet-Massin et al. 2012) or down-sampling (Chen et al. 2004, Evans and Cushman 2009). In each method, many more availability points are sampled than used points (e.g., 10:1). In equal sampling, the available (background) points are repeatedly subsampled to an equal ratio with used points and used to grow multiple RF models, the outputs of which are then averaged. In this study I used an equal sampling method similar to that used by Khalilia et al. (2011) and Reisinger et al. (2021a) and recommended by Valavi et al. (2021). I repeatedly grew RFs with a different random subset of the available data points without replacement until all available points had been compared to the used data, then averaged the resulting RFs to create a form of balanced RF.

Overfitting

While RF is generally not prone to overfitting (Biau 2012), there are many ways to minimize the chance of doing so. One of those is by forcing the RF to build shallow trees so that each node is based on a larger sample size than the default algorithm, rather than making increasingly precise estimates in deep trees with decreasing sample size. I limited the depth of each tree in the RF by allowing the minimum node size to be tuned between 20 and 50 data points.

In RF classification, the default number of candidate covariates randomly selected at each node (*mtry*) is the square root of the total number of covariates. Having relatively few covariates in this study, I allowed *mtry* to vary in model tuning between 3, 4, 5, and 8 randomly selected covariates, which reduces overfitting and produces more stable outcomes (Garzón et al. 2006). Though the RFs grew stable after a few hundred trees, I grew each RF to 1000 trees to be conservative.

Another effective method to minimize the chance of overfitting is cross-validation during model training (Roberts et al. 2017, Liaw and Wiener 2018), which is common in habitat selection studies using RF (Vanbianchi et al. 2017, Heffelfinger et al. 2020, Reisinger et al. 2021b, 2021a, Shanley et al. 2021). I used a seven-fold leave-group-out cross-validation (LGOCV), where the data were grouped by individual sage-grouse (similar to Heffelfinger et al. 2020). As the RF is grown, each tree is trained on data from a random subset of individuals and tested on data from the remaining individuals. Grouping data by individual or meaningful group of individuals helps account for individual variation in habitat selection and minimizes the chance of testing the model's performance on data closely associated with data used to train it (Roberts et al. 2017, Zhang et al. 2019, Aldossari et al. 2021). This step also makes the RF models more similar to the mixed effects GLM used in a simple RSF with individual habitat selection.

Model evaluation

I evaluated model performance both within each study area and across study areas. I first trained each RF using a random sample of 70% of the dataset. Then, I tested the average LGOCV model's capacity to predict the withheld 30% data within the same study area. Because part of this study was focused on the variation in habitat selection, this first step was useful to describe the transferability of models within each study area and provide greater certainty when describing the differences between study areas. I tested each model's capacity to predict the withheld data in every other study area, which provides a truly out-of-sample dataset while still granting insight into ecological processes and the variation in habitat selection across this fragmented range margin. For comparison with the RF models, I performed the same model evaluation across study areas using the RSF models.

Many RF habitat selection studies use the area under the receiver operator characteristic curve (AUC), a measure of the tradeoff between model sensitivity and specificity, to evaluate the model performance. However, AUC has lately been discouraged for evaluating models based on used-available data (see Austin 2007, Lobo et al. 2008, Fieberg et al. 2018, Shabani et al. 2018). Alternatively, the true skill statistic (TSS) is a measure of the model's combined performance in both specificity and sensitivity and has been shown to be appropriate and useful with presence-only data, including when using RF (Allouche et al. 2006, Mi et al. 2017, Shabani et al. 2018, Yudaputra et al. 2020). TSS can theoretically range from -1 to 1, with 0 being a totally uninformative model. To evaluate models, I used the true skill statistic (TSS), in addition to comparing model sensitivity (ability to predict used location points), and the correlation coefficient in a used-habitat calibration, similar to (Fieberg et al. 2018).

Model interpretation

To understand the impacts of the environmental covariates on sage-grouse habitat selection, I used different methods for the RSF and RF models. For the RSFs, I visualized the predicted probability of selection vs avoidance based on model estimates (Manly et al. 2002). For the RFs, I used the R package *pdp* (Greenwell 2017) to calculate partial dependence of each covariate and the R package *rfFC* (Palczewska and Robinson 2015) to calculate feature contribution. Partial dependence measures the marginal effect of a covariate, calculating the predicted outcome in selection vs avoidance across the range of that covariate when the marginal effects of all other covariates in the model are held at their average value. In this study I used partial dependence plots to visualize interactive (two-way) effects on habitat selection. Feature contribution also measures the impact of a covariate on selection, but instead of averaging the effects of other covariates, feature contribution accounts for interactions with other covariates directly (Kuz'min et al. 2011, Palczewska et al. 2014). A positive value of feature contribution indicates that, at that value of a covariate, selection is more likely than avoidance. For example, a feature contribution of 0.1 indicates that selection is 10% more likely than would have been predicted by the RF model without that covariate.

RESULTS

Model performance

Within each study area, the RF models consistently performed better than the RSF models when predicting withheld data measured by TSS, model sensitivity, and used-habitat calibration correlation (Table 4.1). Across all model combinations of study area and season, RF outperformed RSF. In predicting the withheld data from within study areas during model training, the TSS for RF models ranged from 0.579 to 0.767, values in the range suggesting fairly strong predictive performance (Landis and Koch 1977). The RSF models were weaker predicters though still somewhat informative, with TSS values from 0.115 to 0.453. RF models also performed better as measured by sensitivity (0.806 – 0.966) and UHC correlation (0.804 – 0.934) compared to the RSF models' sensitivity (0.564 – 0.776) and UHC correlation (0.610 – 0.839). The RSF and RF models in each study area tended to improve in model performance when using data from within a single season, though for the RSF models in Panguitch during Fall/Winter, and in Summer and Breeding seasons using all study areas, the TSS was slightly lower. The improvements in model performance of RF over RSF were greatest in Bald Hills and Cave study areas. While RF performance was fairly high across all study area – season combinations, RSF performance was notably higher in Panguitch (mean TSS = 0.433) than in the study area with the poorest performance, the Bald Hills (mean TSS = 0.143).

The differences between RF and RSF models were slightly smaller in their capacity to predict data from study areas outside where they were trained (Table 4.2). Still, RF performed better across all combinations of study area, with an average difference in performance of TSS = 0.339, sensitivity = 0.165, and UHC correlation = 0.136. RF model performance was poorer than when tested on withheld data from within study areas, yet still suggested moderate predictive capacity (mean TSS = 0.496, mean sensitivity = 0.699, mean UHC correlation = 0.744). The best performance predicting data in other study areas was in the Cave RF model predicting Bald Hills data (mean of performance metrics = 0.738), followed by Bald Hills predicting Panguitch (mean performance = 0.675), Bald Hills predicting Cave (mean performance = 0.671) and Panguitch predicting Bald Hills (mean performance 0.665). The worst performing RF model was in the Panguitch model predicting Hamlin (mean performance = 0.575).

RSF model performance on predicting data in other study areas was likely only marginally informative (mean TSS = 0.157, mean sensitivity = 0.541, mean UHC correlation = 0.608). The best RSF performance was in the Cave model predicting Panguitch (mean performance = 0.499), Bald Hills predicting Panguitch (mean performance = 0.495), Cave predicting Hamlin (mean performance = 0.475), and Bald Hills predicting Cave (mean performance = 0.461). The RSF prediction with poorest performance was in Bald Hills predicting Hamlin (mean performance = 0.382).

The greatest difference in model performance between RF and RSF models was when using the model built in Cave to predict Bald Hills data (difference in mean performance = 0.308), in Hamlin predicting Cave (difference in mean performance = 0.264), and Hamlin predicting Panguitch (difference in mean performance = 0.251). Using RF instead of RSF made the smallest difference in Cave predicting Hamlin (difference in mean performance = 0.174).

Covariate impacts

After excluding the variables with excessive collinearity or contribution to variance inflation, the RSF model with the lowest AICc for each study area included distance to trees (TREEDIST) and a combination of sagebrush cover and topographic metrics at several scales (Table 4.3). In each study area there was a decreasing probability of selection with increasing topographic heterogeneity and slope, but the effect of topographic position varied in the strength and trend (Figure 4.2). The probability of selection increased with increased topographic position in Hamlin Valley and the Bald Hills. In Cave Valley there was a weaker increase in probability of selection with increased topographic position index within 400 m and in Panguitch selection slightly decreased with increasing topographic position (TPI400: $\beta = -0.02$). In each study area, the probability of selection decreased as tree density increased in both 400 m and 800 m windows and increased with the distance from trees (Figure 4.3).

The RF models detected many of the same trends as the simple RSFs, though there were important differences between their findings; the RFs showed notable nonlinear effects of tree cover, sagebrush patch characteristics, and topography compared to the available habitat that the RSFs did not. While both RSF and RF indicated that selection was less likely near trees and with greater tree cover, the RF models suggest that there are particular levels of tree cover where sage-grouse selection is higher than would be predicted by the RSFs (Figure 4.4). For the RFs in each study area, the probability of selection was highest at very low levels of tree cover. Yet the decrease in selection probability was inconsistent; in each study area sage-grouse were less likely to select habitat with 10 – 18% tree cover in an 800 m window (TREEDEN800, Figure 4.4a) than they were to select habitat with greater tree cover. That threshold varied across study areas. Similarly, sage-grouse in all study areas but Hamlin were more likely to select habitat with 30 – 40% tree cover than 10% cover. There was also a nonlinear impact of distance to trees, where probability of selection generally increased with greater distance to trees in all study areas but Panguitch, but fell again or leveled off above a distance specific to that study area (Figure 4.4). For example, in Cave the probability of selection was greater at approximately 500 m from trees than at 1000 m. In Panguitch, selection probability was highest near trees and slowly decreased with distance to trees, with avoidance becoming more likely than selection at distances greater than 250 m.

The RF models showed similar nuance in the impact of topography as they did for tree cover. In all study areas but the Bald Hills, the probability of selection was highest at a moderate level of topographic heterogeneity than in homogeneous topography (Figure 4.5). In the Bald Hills, there was a generally decreasing trend in selection with increasing heterogeneity. Similarly, in the Bald Hills selection probability was higher in moderately high topographic position (e.g., small ridges) than in flat or low terrain, but the opposite was true in the three other study areas. The RFs also indicate that in some conditions, sage-grouse were more likely to select areas close to trees than would be predicted by the RSFs. When sage-grouse were close to trees (< 100 m), they were more likely to select terrain that was lower than the terrain around it and in sagebrush patches of greater core area and contiguity (Figure 4.6).

Seasonality

As in the results across study areas, the seasonal RSF models tended to find the same general trends as the RFs, but did not detect some of the perturbations within seasonal trends or showed weak effects in the opposite direction. While both the RF and RSF models showed a generally decreasing probability of selection with increased tree density for each season, especially above about 12% tree cover, the RSF models (Figure 4.7) did not detect the same peaks in selection between 30% and 40% cover in each season that the RF models did (Figure 4.8). Instead, the RSF models showed a weaker effect of increasing tree density in summer than in the fall/winter or breeding seasons. There was also a variation in seasonal effects of tree cover across study areas. The RSF models showed that in Fall/Winter and Breeding seasons, probability of selection decreased with increasing tree cover in all study areas, yet during Summer selection probability increased in the Bald Hills and Cave study areas (Figure 4.9). The RF models suggested a similar pattern, though they showed a local peak in selection in Bald Hills, Cave, and Panguitch during Summer at 30 – 45% tree cover, followed by rapid trends toward avoidance with greater tree density (Figure 4.10).

Similarly, the RSF models did not detect the same thresholds in sagebrush patch size and configuration (Figure 4.11) as the RF models (Figure 4.12). The RFs detected the strongest selection for higher sagebrush core area index (CAI) and patch contiguity (CONTIG) in fall/winter, with an apparent threshold for increasing selection above CAI = 45% and CONTIG = 0.75 (Figure 4.12), while the RSFs showed a weak avoidance for high values of those sagebrush variables in fall/winter (Figure 4.11). The RSFs predicted weak selection for higher sagebrush CAI and CONTIG in summer and strong selection in the breeding season, while the RFs suggested a weak effect until a threshold, above which in summer selection decreased and in the breeding season increased. Further, both RSF (Figure 4.13) and RF (Figure 4.14) models showed different seasonal selection for sagebrush patches across study areas. Both showed that during summer, sage-grouse were less likely to select areas of high sagebrush patch contiguity in all study areas but Panguitch, though that trend in Panguitch was not as strong in the RFs.

DISCUSSION

Model performance

The RF models performed very well within study areas, and moderately well across all study areas and seasons. Although the RF model across study areas selected similar variables, the results were not as robust as the RF for any single study area. RF models consistently performed better than the conventional RSF model of the same study area – season combination.

The RF models also performed well in predicting data from outside the study area where they were trained, suggesting a moderate degree of model transferability. Most notably, the RF models were consistently better in predicting out-of-sample data than the RSF models, despite the fact that other studies have reported poor performance and potential overfitting with a standard RF (Shabani et al. 2016). Despite past findings that RF has limitations when predicting out of sample data, many other studies have shown it has equal or superior performance in creating accurate range maps and predicting out of sample data compared to other methods, including with rare species and low sample size (Mi et al. 2017). In my study, while there was variation in which variables were selected as the most important across study areas, as well as among the specific thresholds and magnitudes of their impacts, each study area’s model suggests similar conclusions.

In both RF and RSF, many of the same variables were selected by the models as important, but with differences in their effects. For example, increasing tree density within 800 m (TREEDEN800) in RF models in every study area had a generally negative effect on selection, though nonlinearly and with different small perturbations in each. For example, in each study area there was a local minimum in selection between 10% and 18% tree cover within 800 m. Yet that minimum varied across study areas, as did the rate of increase in selection at increasing levels of tree cover. This suggests while sage-grouse respond to many of the same habitat features in the region of their southern range margin, they likely face different limiting factors depending on the local conditions. The ability to predict habitat selection across study areas was greater with RF than RSF models, similar to Shoemaker et al. (2018) and Shanley et al. (2021). Therefore, while grouse likely respond to many of the same cues across their range (e.g., sagebrush cover, mesic habitat), regional variation in their environment drives them to respond to different thresholds in those important habitat characteristics.

There is growing evidence for the benefits of using machine learning techniques like RF in habitat selection studies (Cai et al. 2014, Severson et al. 2017b, Shoemaker et al. 2018, Reisinger et al. 2021a, Shanley et al. 2021). When designed appropriately with biologically relevant variables and scales, RF models may be especially useful for place-based analyses, both descriptive and predictive. Thresholds and other nonlinear relationships are common in ecosystems and my findings demonstrate the need to identify how habitat selection varies across species' range. RF models are not prone to overfitting and deal better with both autocorrelation and variable correlation than many traditional methods while not sacrificing model transferability (Cutler et al. 2007, Farrell et al. 2019). Compared to other means of modeling nonlinear effects like GAMs, RF is also likely better able to detect complicated relationships and interactions, performs better predicting out-of-sample data, and may be especially useful for studying habitat specialists (Kosicki 2020, Valavi et al. 2022). It will be important to incorporate RF and other nonparametric methods into ecological research, especially where there are suspected nonlinear effects and region- or locality-specific thresholds. While RSF should continue to play an important role in analyzing habitat selection and other used-available data, especially at a broad scale (e.g. state or range-wide), it may be especially important to implement RF or other machine learning methods at range edges, in fragmented habitat, or in other marginal habitat. Continued focus at both regional and local scales will better inform conservation and management and flexible methods like RF can be a valuable addition to HSAs.

Implications

It is well documented that sage-grouse populations are negatively impacted and distributions reduced by tree cover in their environment. My RSF models supported that finding. However, the RF models demonstrated greater nuance in sage-grouse response to tree cover, suggesting that there are conditions in which sage-grouse appear to tolerate greater tree cover or being nearer trees than is usually reported. In this region of sage-grouse distribution, encroachment by pinyon-juniper forest into sagebrush habitat is common. It may be that, in these study areas that are already fragmented by mountains and marginal habitat (West 1983a, Miller and Eddleman 2001), sage-grouse have less available habitat in which to escape from the threats posed by tree cover and instead select habitat that provides visual cover from potential avian predators in those trees (Beers and Frey 2022a). The RF models suggest that sage-grouse may use both topography and contiguous sagebrush habitat as cover when they are near trees. Dinkins et al. (2014) also found that sage-grouse selected moderately rugged terrain and similarly suggested that behavior was to use topography as visual cover from avian predators. My simple RSF models did not detect that nonlinear effect of topography. While methods exist to model nonlinear relationships within RSFs or GAMs, they are likely more difficult for many users to implement than RF and do not perform as well in predicting out-of-sample data (Kosicki 2020, Valavi et al. 2022).

Our results also support the utility in exploring new methods to evaluate animal habitat selection, especially to account for local variation and better inform decision-making. The RF models performed outperformed the simple RSF models by each metric and allowed me to identify important interactions and nonlinear effects that were not detected by the RSF models. My findings imply local-scale variation in habitat selection exists that could inform sage-grouse and sagebrush habitat management and conservation decisions. This suggests that land managers should prioritize conifer removal treatments in flatter terrain and areas of lower sagebrush contiguity, where sage-grouse are unable to use those features as visual cover from avian predators (Beers and Frey 2022a). Were I to have used only simple RSFs in this study, I would have concluded that sage-grouse avoid rugged terrain and habitat near trees and would not have detected those details that can inform more precise, place-based management and conservation. The RF models may help identify potentially-critical thresholds in sage-grouse habitat selection that the RSFs did not detect and reinforce the need to study habitat selection and requirements at both local and regional scales.

There are potential pitfalls in using RF to study habitat selection, especially due to class overlap and imbalance and clustered data that could either obscure or exaggerate trends. Habitat selection data often has autocorrelation and dependency structures that likely make the most basic form of RF ineffective (Roberts et al. 2017). However, if steps are taken to understand the data’s structure and account for these issues, its implementation can yield a nuanced and precise understanding (Valavi et al. 2021) and RF should be considered among the tools available to practitioners studying wildlife-habitat associations.

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FIGURES AND TABLES

Table 4.1. Performance of resource selection function (RSF) and random forest (RF) models in predicting data withheld during model training. Model performance was evaluated using the true skill statistic (TSS), model sensitivity, and correlation in a used-habitat calibration (UHC).

		Method					
		Resource Selection Function			Random Forest		
Study Area	Season	TSS	Sensitivity	UHC correlation	TSS	Sensitivity	UHC correlation
All	All	0.143	0.609	0.689	0.579	0.806	0.867
All	Fall/Winter	0.220	0.616	0.671	0.635	0.846	0.871
All	Breeding	0.124	0.594	0.703	0.604	0.818	0.849
All	Summer	0.115	0.586	0.724	0.589	0.804	0.881
Bald Hills	All	0.118	0.622	0.610	0.707	0.842	0.890
Bald Hills	Fall/Winter	0.175	0.633	0.655	0.767	0.952	0.924
Bald Hills	Breeding	0.129	0.659	0.678	0.719	0.966	0.934
Bald Hills	Summer	0.148	0.586	0.662	0.720	0.934	0.912
Cave	All	0.144	0.564	0.644	0.594	0.811	0.804
Cave	Fall/Winter	0.183	0.665	0.702	0.642	0.884	0.867
Cave	Breeding	0.341	0.675	0.725	0.638	0.871	0.817
Cave	Summer	0.155	0.597	0.693	0.629	0.855	0.811

Hamlin	All	0.224	0.618	0.592	0.586	0.826	0.886
Hamlin	Fall/Winter	0.285	0.660	0.764	0.621	0.861	0.897
Hamlin	Breeding	0.270	0.681	0.749	0.648	0.849	0.892
Hamlin	Summer	0.244	0.659	0.774	0.61	0.825	0.906
Panguitch	All	0.429	0.755	0.827	0.595	0.834	0.873
Panguitch	Fall/Winter	0.401	0.776	0.832	0.603	0.844	0.885
Panguitch	Breeding	0.453	0.739	0.805	0.655	0.863	0.916
Panguitch	Summer	0.449	0.758	0.839	0.700	0.835	0.905

Table 4.2. Performance of resource selection function (RSF) and random forest (RF) models in predicting data in all study areas other than that used for model training. Model performance was evaluated using the true skill statistic (TSS), model sensitivity, and correlation in a used-habitat calibration (UHC).

		Method					
		Resource selection function			Random Forest		
Model training	Model testing	TSS	Sensitivity	UHC correlation	TSS	Sensitivity	UHC correlation
Bald Hills	Cave	0.114	0.589	0.679	0.485	0.802	0.727
Bald Hills	Hamlin	0.111	0.492	0.544	0.442	0.663	0.709
Bald Hills	Panguitch	0.189	0.601	0.694	0.481	0.746	0.798
Cave	Bald Hills	0.137	0.526	0.628	0.528	0.883	0.803
Cave	Hamlin	0.207	0.612	0.605	0.545	0.642	0.759
Cave	Panguitch	0.215	0.632	0.651	0.49	0.676	0.724
Hamlin	Bald Hills	0.107	0.653	0.55	0.507	0.723	0.75
Hamlin	Cave	0.122	0.501	0.538	0.496	0.739	0.718
Hamlin	Panguitch	0.232	0.467	0.533	0.433	0.79	0.761
Panguitch	Bald Hills	0.164	0.455	0.698	0.568	0.688	0.738
Panguitch	Cave	0.149	0.46	0.65	0.51	0.547	0.741
Panguitch	Hamlin	0.135	0.498	0.523	0.463	0.566	0.695

Table 4.3. Variables included in the best fit resource selection function (RSF) model in each study area, the most important of those variables, the difference in AICc from a null model, and the conditional R^2. The potential variables included 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	Variables included	Most important variable	ΔAICc	Conditional R^2
Bald Hills	All	TPI400 + THI400 + CAI + Slope + TREEDIST + TREE400	TREEDIST	10645.8	0.21
Bald Hills	Fall/Winter	THI50 + TPI400 + THI400 + CAI + Slope + TREEDIST + TREEDEN400	TREEDIST	7934.1	0.366
Bald Hills	Breeding	TPI200 + TPI400 + THI400 + CAI + TREEDIST + TREEDEN400	TREEDIST	4696.5	0.361
Bald Hills	Summer	TPI400 + THI400 + CAI + Slope + TREEDIST + TREEDEN400	TREEDIST	1537.6	0.123
Cave	All	THI200 + CAI + Slope + TREEDIST + TREEDEN400	CAI	628.3	0.107
Cave	Fall/Winter	TPI200 + THI400 + CAI + TREEDIST + TREEDEN400	CAI	211.2	0.194
Cave	Breeding	THI50 + THI400 + CONTIG + TREEDIST + TREEDEN800	TREEDIST	1151.2	0.782
Cave	Summer	TPI50 + TPI400 + THI400 + CONTIG + TREEDIST + TREEDEN400	CONTIG	470.9	0.184

Hamlin	All	TPI400 + THI400 + CAI + TREEDIST + TREEDEN400	TREEDEN400	5333.9	0.276
Hamlin	Fall/Winter	TPI400 + THI400 + CONTIG + TREEDIST + TREEDEN400	TREEDEN400	3393.6	0.608
Hamlin	Breeding	TPI400 + THI400 + CAI + Slope + TREEDIST + TREEDEN400	TREEDEN400	2151.4	0.704
Hamlin	Summer	TPI400 + THI400 + CAI + Slope + TREEDIST + TREEDEN400	TREEDEN400	2359.9	0.263
Panguitch	All	TPI200 + THI200 + CAI + TREEDIST + TREEDEN400	CAI	6208.7	0.469
Panguitch	Fall/Winter	TPI400 + THI400 + CAI + TREEDIST + TREEDEN800	TREEDEN800	4876	0.606
Panguitch	Breeding	TPI400 + THI400 + CONTIG + Slope + TREEDIST + TREEDEN400	CONTIG	2349.9	0.512
Panguitch	Summer	TPI200 + THI400 + CAI + TREEDIST + TREEDEN400	CAI	749.3	0.267

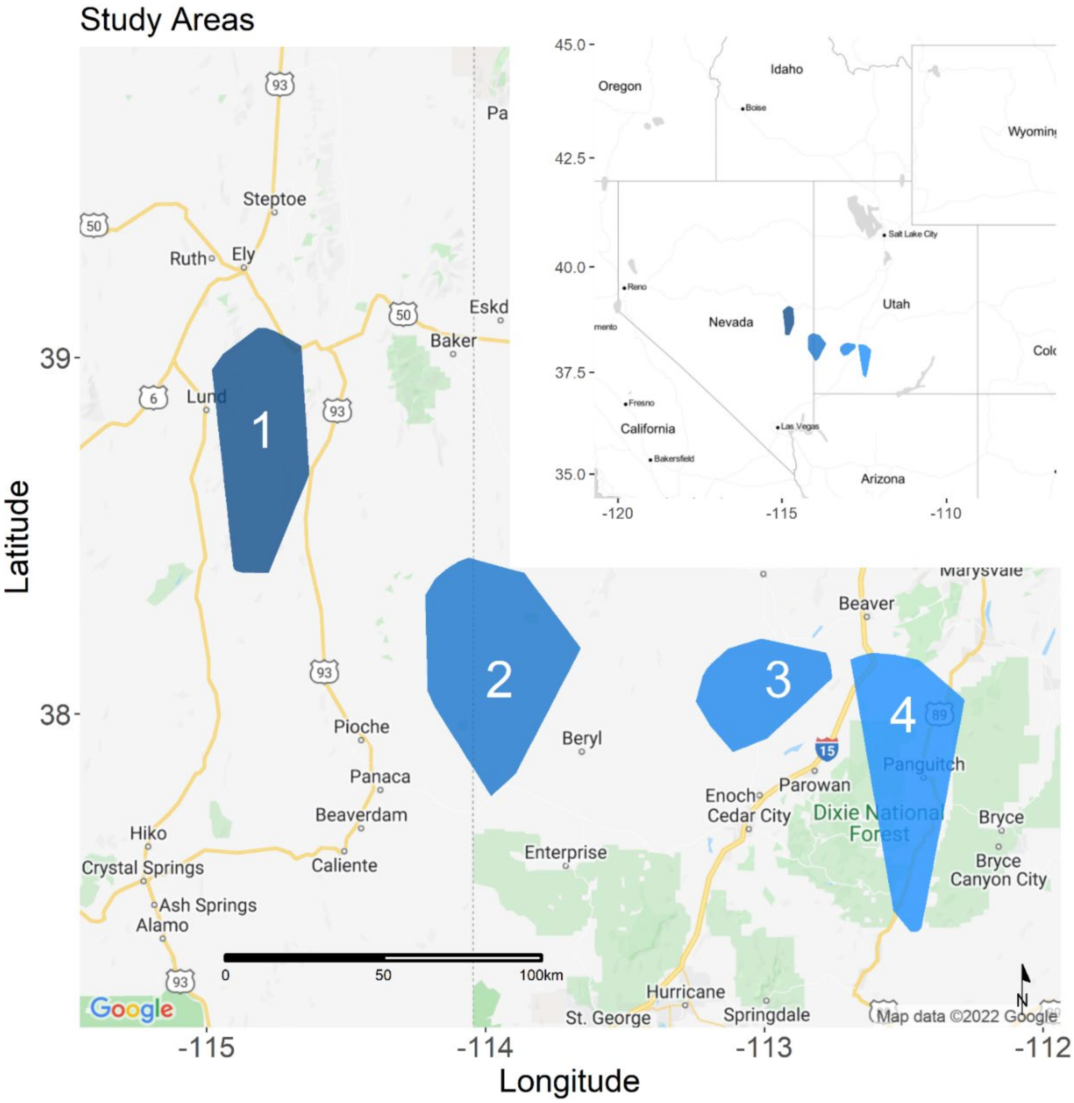

Figure 4.1. Four study areas and their context in Utah and Nevada, drawn here by a minimum convex polygon around the data points used in my analyses. Study areas are 1) Cave/Steptoe Valleys, 2) Hamlin Valley, 3) Bald Hills, and 4) Panguitch.

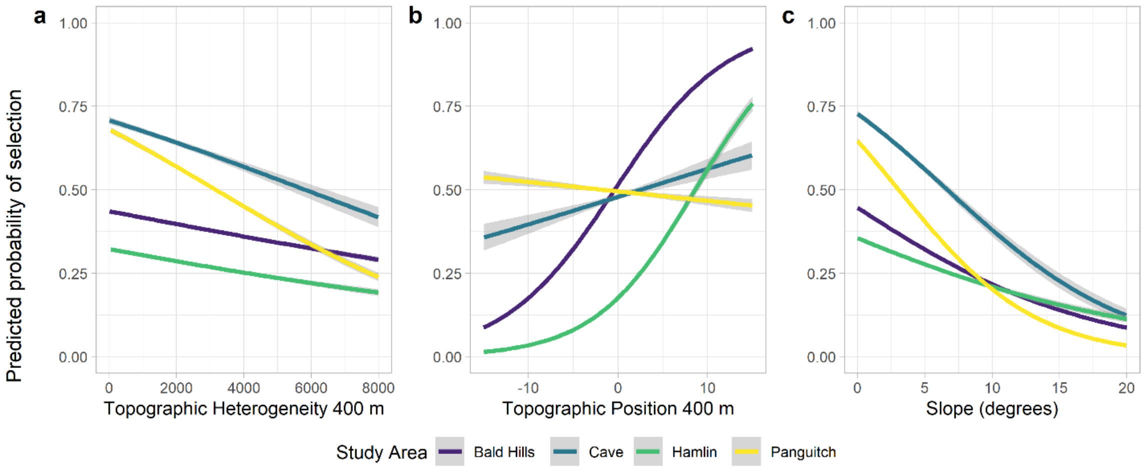

Figure 4.2. RSF predicted probability of habitat selection by sage-grouse in each study area in response to a) topographic heterogeneity in a 400 m window (THI400), b) topographic position compared to a 400 m window (TPI400), and c) slope.

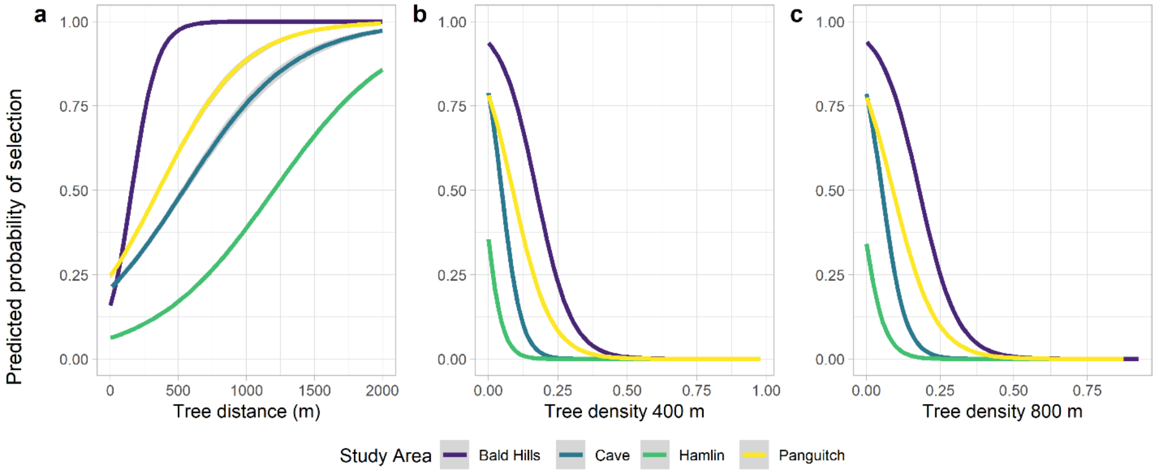

Figure 4.3. RSF predicted probability of habitat selection by sage-grouse in each study area in response to a) distance to tree cover (TREEDIST), b) density of tree cover within 400 m (TREEDEN400), and c) density of tree cover within 800 m (TREEDEN800).

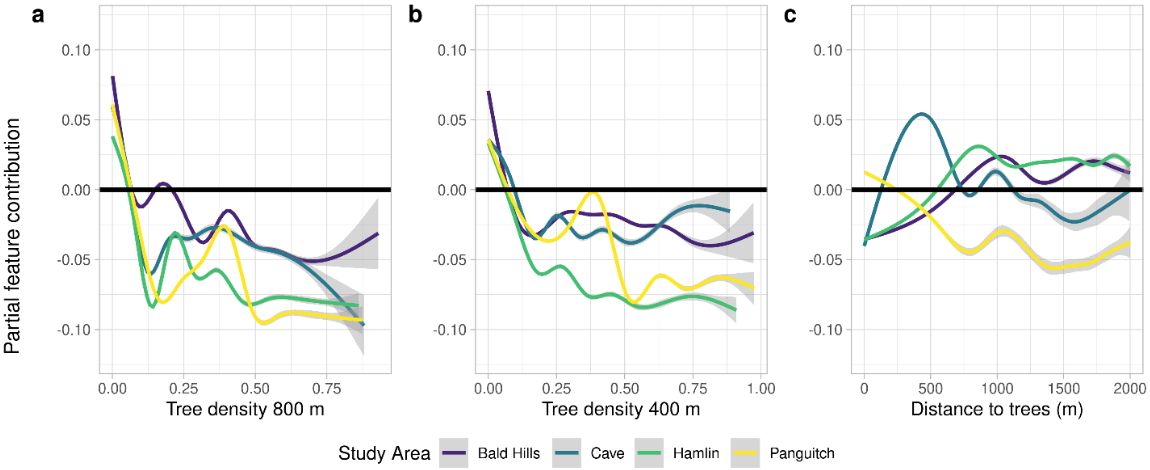

Figure 4.4. Feature contribution[1] of three variables of tree cover in models across four study areas. Panel a) shows the contribution of density of treed pixels in an 800 m radius (TREEDEN800), panel b) shows the contribution of density of treed pixels in a 400 m radius (TREEDEN400), and panel c) shows the contribution of the distance to trees (TREEDIST).

[1] Feature contribution measures how a variable impacts the random forest model's prediction of a point's used vs available status at each value of that variable. A positive value indicates a greater probability of the point being "used" compared to the prediction made by the rest of the model. The solid black line at feature contribution = 0 indicates the point at which selection and avoidance are equally likely.

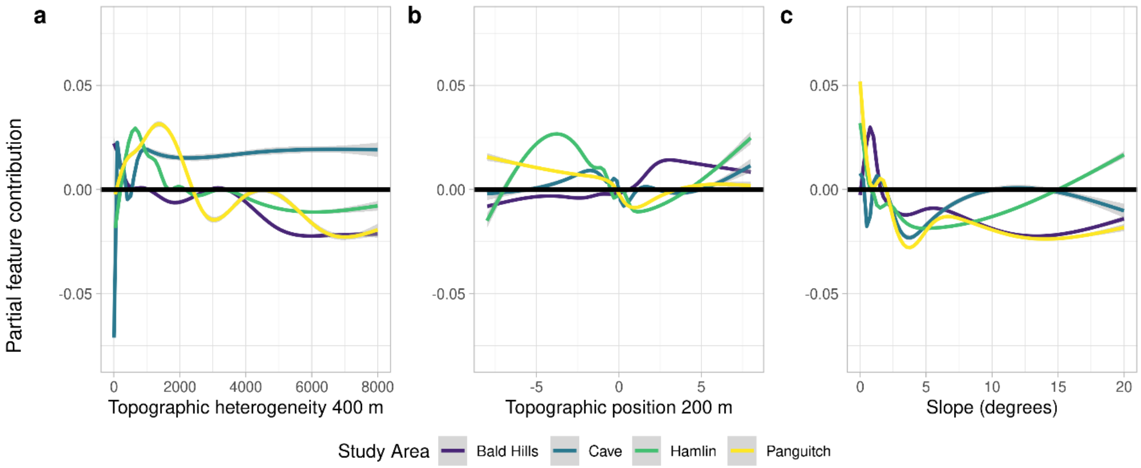

Figure 4.5. Feature contribution to RF model results of three topographic variables in the models across four study areas. Panel a) shows the impact of topographic heterogeneity within a 400 m radius (THI400), panel b) shows topographic position compared to a 200 m radius (TPI200), and panel c) shows topographic slope.

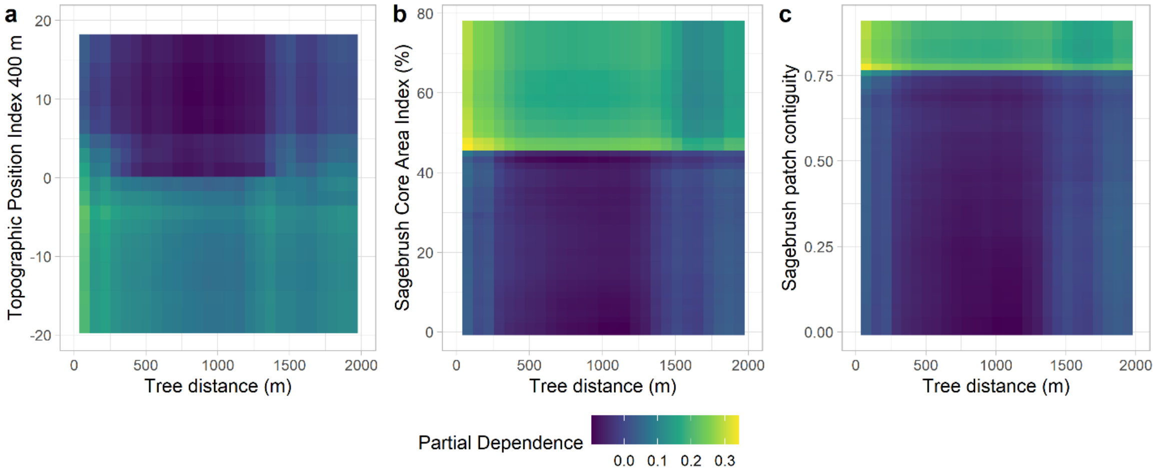

Figure 4.6. Partial dependence[1] of a) topographic position index within a 400 m radius (TPI400), b) sagebrush core area index (CAI), and c) sagebrush patch contiguity (CONTIG) with data from all four study areas.

[1] Partial dependence measures the impact of one variable on the predicted outcome (here, probability of selection) of the response in the RF models. A higher value corresponds to a higher probability of selection.

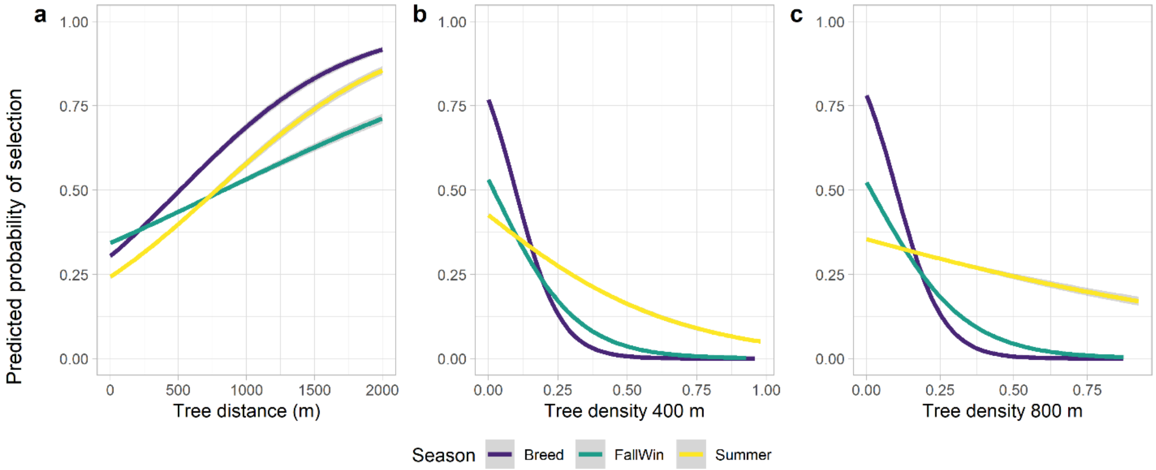

Figure 4.7. RSF predicted probability of habitat selection by sage-grouse in each season in response to a) distance to tree cover (TREEDIST), b) density of tree cover within 400 m (TREEDEN400), and c) density of tree cover within 800 m (TREEDEN800).

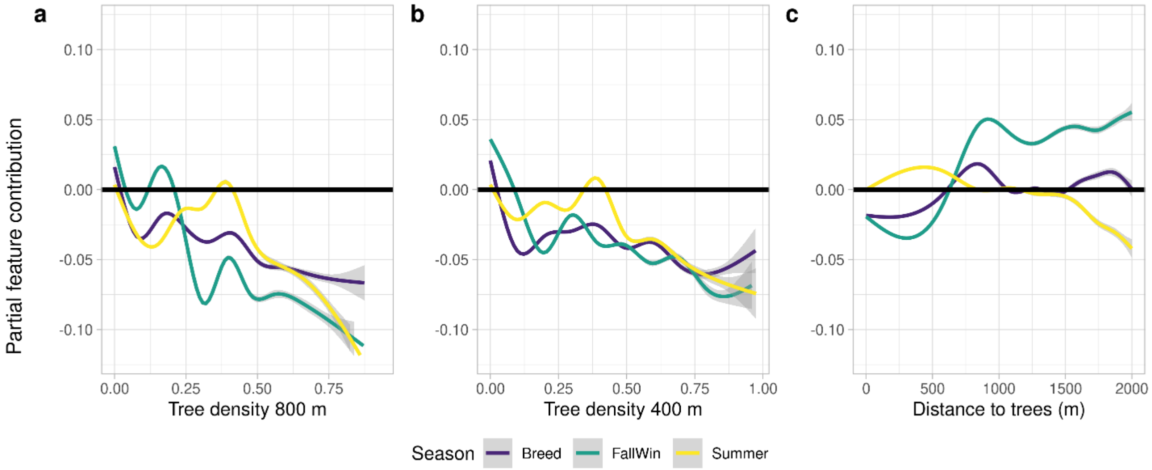

Figure 4.8. Feature contribution to RF model results in each season of a) density of treed pixels within 800 m (TREEDEN800), b) density of treed pixels within 400 m, and c) distance to trees (TREEDIST).

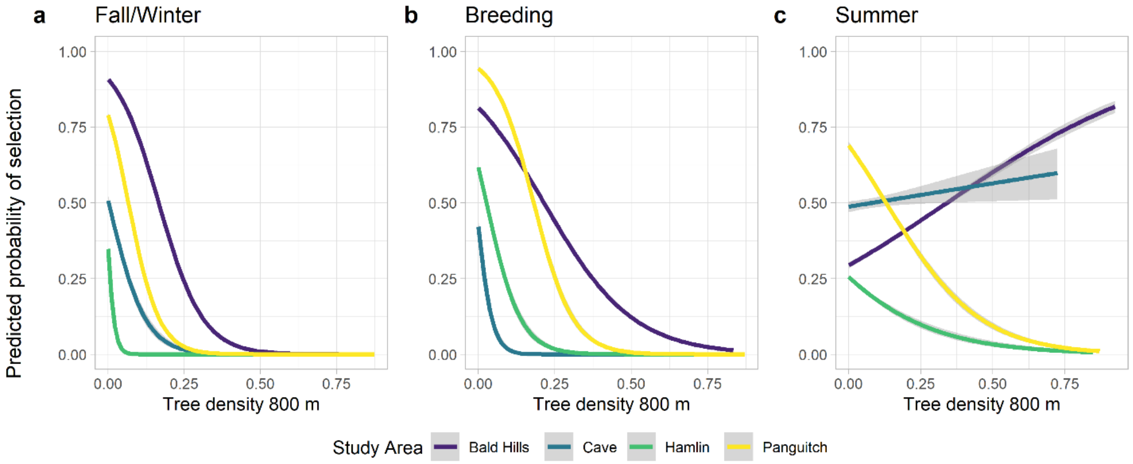

Figure 4.9. RSF predicted probability of habitat selection by sage-grouse in each study area in response to density of tree cover within 800 m (TREEDEN800) during a) Fall/Winter, b) Breeding, and c) Summer seasons.

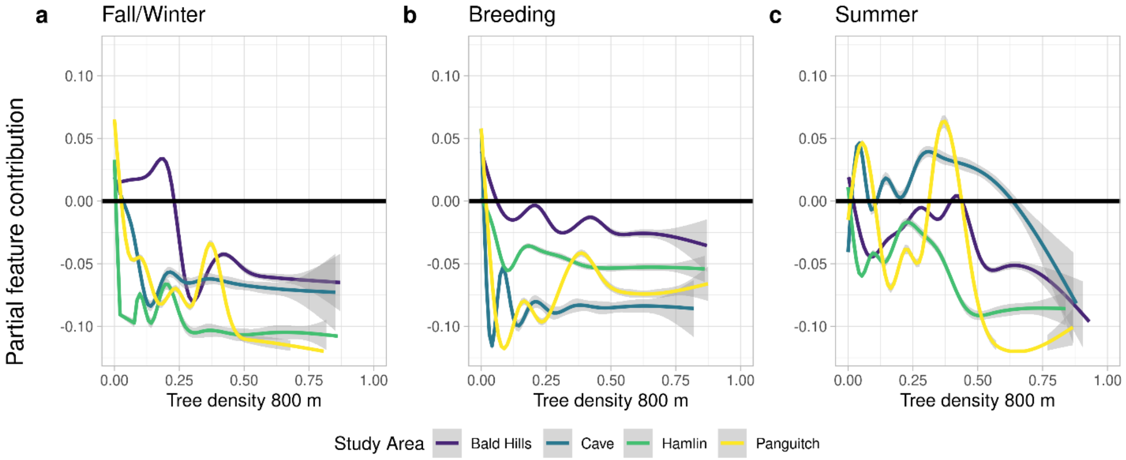

Figure 4.10. Figure contribution to RF model results in each study area of tree density within 800 m (TREEDEN800) in a) Fall/Winter, b) Breeding, and c) Summer seasons.

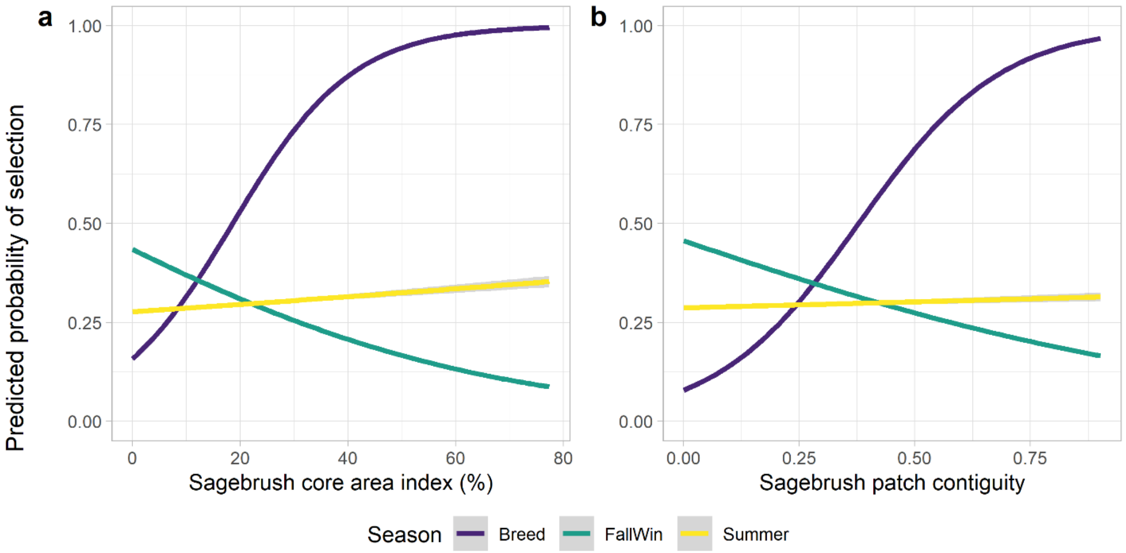

Figure 4.11. RSF predicted probability of habitat selection by sage-grouse in each season in response to a) sagebrush patch core area index (CAI) and b) sagebrush patch contiguity (CONTIG).

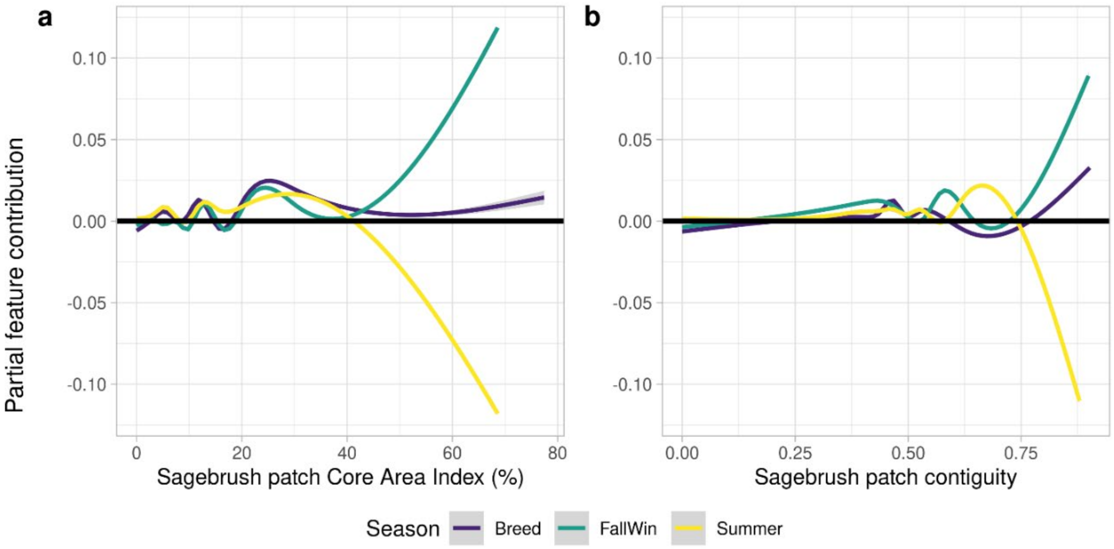

Figure 4.12. Feature contribution to RF model results in each season of a) sagebrush core area index (CAI) and b) sagebrush patch contiguity (CONTIG).

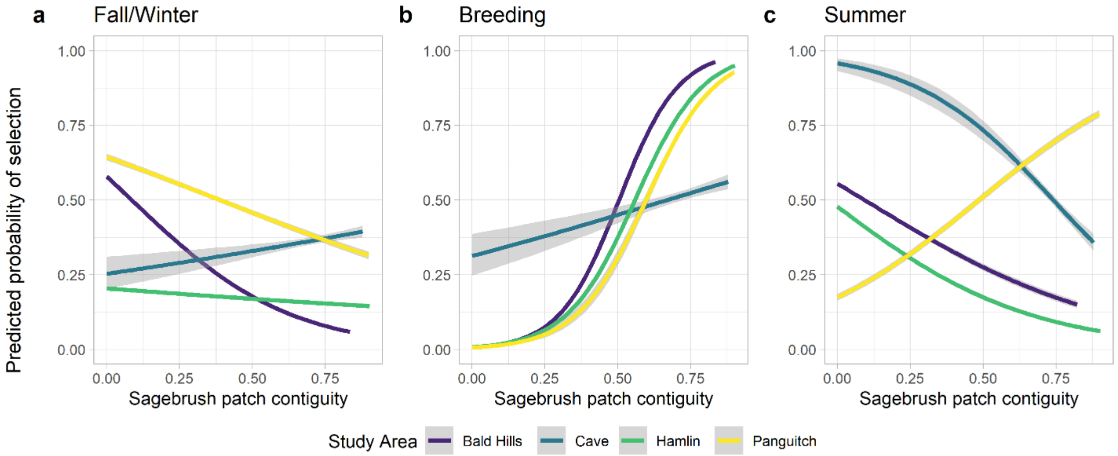

Figure 4.13. RSF predicted probability of habitat selection by sage-grouse in each study area in response to density of sagebrush patch contiguity (CONTIG) during a) Fall/Winter, b) Breeding, and c) Summer seasons.

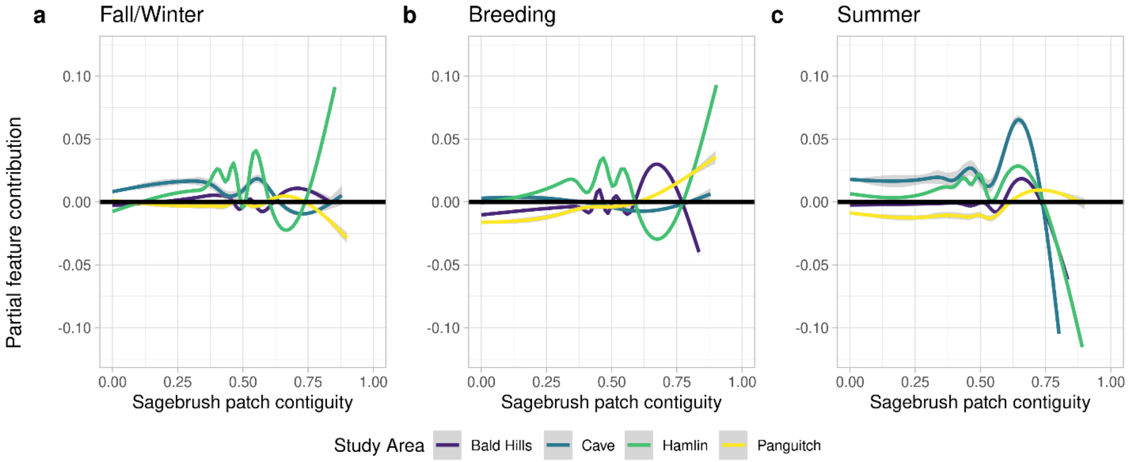

Figure 4.14. Feature contribution to RF model results in each study area of sagebrush patch contiguity (CONTIG) during a) Fall/Winter, b) Breeding, and c) Summer seasons.

CHAPTER V

CONCLUSIONS

As habitat specialists that rely on the quality and connectivity of sagebrush at multiple scales, sage-grouse are an imperiled denizen of sagebrush ecosystems, which are among the most threatened ecosystems in North America (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004, Wisdom et al. 2005). Ongoing efforts to understand and conserve sage-grouse and their habitat are emblematic of many of the conservation issues of North America, as they require cooperation across political boundaries and the contribution of a wide variety of stakeholders. Understanding the varied challenges that sage-grouse face and the barriers to their conservation may illustrate many issues of land management and wildlife conservation more generally.

Greater sage-grouse face a variety of threats to their persistence, the greatest of which is habitat loss (Braun 1998, Schroeder et al. 2004). Yet the factors limiting sage-grouse habitat vary across their distribution, and it is difficult to implement a single directive for their management. In order to understand the factors likely to drive future habitat loss and extirpations, it is important to study their habitat selection across their distribution, but especially in areas of fragmented and poor-quality habitat. This will help us understand the environmental factors limiting their distribution and those that are likely to drive extirpations in the future. In this dissertation, I have conducted work aimed at describing the mechanisms limiting sage-grouse habitat selection at their southern range margin and providing more actionable knowledge for their conservation and management.

With variable threats to sage-grouse and their habitat, it is critical to analyze the most important habitat characteristics and limiting factors in different portions of their distribution. We know already that, while sage-grouse generally seek the same habitat (Aldridge et al. 2008), there are different climatic and landscape conditions across their distribution that present different challenges and drive the need for management that varies regionally (Doherty et al. 2016, Coates et al. 2021). In the southern Great Basin, sage-grouse habitat tends to be more xeric and more fragmented than in the core of their distribution (Miller and Eddleman 2001). The southern range margin provides a potential natural laboratory to evaluate the factors limiting sage-grouse habitat selection and, by extension, distribution. That knowledge can inform future conservation and management where these marginal conditions may eventually become more prevalent.

In Chapter 2, I analyzed the impact of land cover and topography on sage-grouse habitat selection at local scales and how those impacts varied across four study areas using a random forest (RF) model. I found that sage-grouse may use sagebrush patches and topography as shelter from the perceived predation risk presented by conifers. In these findings, I have identified a nuance in the relationship between sage-grouse and their habitat, wherein they will select (or tolerate) tree cover under some conditions. This has important implications for how sage-grouse respond to conifer encroachment into sagebrush habitat. While it does not suggest that conifer encroachment is not a threat to sage-grouse, it does imply that sage-grouse exploit dense sagebrush and topography to continue using habitat that might otherwise be inaccessible because of the threat of predation.

However, knowing that sage-grouse are threatened by and tend to avoid tree cover in other areas of their range, it is unclear why I found that sage-grouse will select areas of greater tree cover in some conditions. In Chapter 3, I sought to test a potential mechanism. Ongoing climate change threatens sagebrush habitat, especially in the southern Great Basin, the southern end of sage-grouse distribution (Kleinhesselink and Adler 2018, Renwick et al. 2018). Sage-grouse in this region are likely to face conditions that are more xeric and with less sagebrush cover. So, while it appears that sage-grouse exploit sagebrush cover and topography to make tree cover less threatening, they are likely to have less capacity to do so in the future. It is also clear that sage-grouse in more xeric habitats are more prone to extirpation and climate appears to be an important factor, for which they may be both direct and indirect causes; higher temperature and lower precipitation drive population decreases, likely due to impacts on both sagebrush and mesic habitat (Holloran et al. 2005, Aldridge et al. 2008, Wisdom et al. 2011, Acevedo 2021).

In addition to the impacts of climate change on sagebrush cover, sage-grouse are also likely to face threats from direct thermal stress, as the forecasted impacts on sagebrush communities are likely to reduce their thermal buffering capacity compared to intact sagebrush systems (Anthony et al. 2020). However, no study of which I am aware has demonstrated how thermal stress impacts sage-grouse habitat selection. While some have shown an impact on other gallinaceous species (Hovick et al. 2014, Rakowski et al. 2019), it is crucial to understand when and where thermal stress impacts sage-grouse and how to best conserve essential thermal refuge habitat. This will inform and add nuance to decision-making based on the variety of threats that sage-grouse face, as thermal stress could create cryptic habitat fragmentation and explain patterns of habitat selection and suitability in some areas of their distribution. In Chapter 3, I used temperature from *in situ* data loggers to describe how and when temperature drives sage-grouse habitat selection across the landscape and throughout the year at their warm, southern range margin.

I found that sage-grouse respond to the most extreme temperatures by selecting habitat with greater tree cover and nearer to trees in the study area with hotter mean temperatures and in dense sagebrush in the study area with cooler mean temperatures. This suggests that sage-grouse are threatened by direct thermal stress and respond to the risk of it by using vegetation cover for thermal refuge. Where it is available, they appear to select dense sagebrush cover. However, at higher temperatures and with less contiguous sagebrush cover, they exploit the shade of tree cover to minimize thermal stress. My findings suggest that when exposed to extreme heat, sage-grouse are compelled to select habitat that could incur greater risk of depredation by avian predators due to the presence of tree cover (Coates et al. 2017, Prochazka et al. 2017).

Studying wildlife-habitat relationships at the multiple scales at which they function can inform our understanding of the mechanisms driving wildlife distributions and population processes. In addition to efforts at larger scales, studying habitat selection by individuals within their home ranges can help define the environmental factors impacting their distribution and function within the ecosystem. For two decades, resource selection functions (RSFs) have been the most common means of analyzing habitat selection and continue to be an invaluable tool for basic and applied research. However, there is growing recognition that methods like RSF may have some limitations when applied to ecological data where nonlinear effects and interactions are common (Recknagel 2001, Elith et al. 2006a, Mi et al. 2017, Valavi et al. 2022). Therefore, it is important to test other methods for analyzing wildlife habitat selection, including their means to both evaluate environmental effects and predict selection in new areas. One of the methods recently used for habitat selection is random forest (RF), a machine learning method that does not assume sample independence, is less constrained by multicollinearity, and is easier to fit to nonlinear relationships and interactions.

In Chapter 4, I analyzed sage-grouse habitat selection across four study areas and three ecologically relevant seasons to compare the effectiveness of RSF and RF. I implemented a RF modeling procedure optimized to minimize the chance of overfitting and mitigate the issues of class imbalance and overlap (Valavi et al. 2021). I also conducted a typical RSF by building generalized linear mixed models for the same study areas and seasons using individual sage-grouse as a random effect. I found that RF models outperformed simple RSF models in their capacity to describe ecological relationships and detect potentially critical interactions and thresholds.

While there was some agreement in ecological findings between the two types of model, the RF models demonstrated important nonlinear effects, including that sage-grouse select areas of greater tree cover and areas closer to trees than predicted by the RSF models. They also indicated potential mechanisms that lead sage-grouse to select habitat close to trees, as sage-grouse were most likely to select that habitat when there was also more contiguous sagebrush cover and moderately rugged terrain, which they may use as visual cover from avian predators using trees. The RSF models did not show that important result. Further, I found that the RF models had a greater capacity to predict data from the other study areas than the RSF models, which shows that the RF models were both more precise and transferable. My findings provide new evidence for sage-grouse selecting habitat near trees, despite the known risk posed by tree cover. While other research has detected sage-grouse selecting habitat nearer trees than expected (Dinkins et al. 2014), my research builds on that finding and suggests a potential means to foster more suitable habitat in areas where conifer encroachment could limit sage-grouse.

CONSERVATION AND MANGAGEMENT IMPLICATIONS

In the preceding chapters, I sought to identify the features of the landscape that drive their habitat selection at the southern edge of sage-grouse distribution, analyze the choices they are likely to make in response to potential threats, and test an alternative method to better inform their conservation. My findings provide ecological nuance for our understanding of sage-grouse habitat needs and actionable information for their conservation and management. In Chapter 2, I found that in some conditions, sage-grouse select habitat nearer to trees than expected and do so in areas where they can use sagebrush and topography as visual cover from potential avian predators. This suggests that in a region where encroaching conifer cover threatens sage-grouse habitat, managers should prioritize conifer removals in flat, open habitat with little sagebrush cover where there is little refuge in which sage-grouse could seek shelter. In Chapter 3, I found that sage-grouse likely select habitat nearer to trees and with greater tree cover during times of extreme heat when sagebrush cover is inadequate shade. When they face thermal stress, sage-grouse are likely forced to select risky habitat where they are more exposed to the risk of predation. To act on this knowledge, where they are exposed to extreme heat land management for sage-grouse may be able to provide suitable microhabitat by leaving clusters of trees for shade, especially in rugged terrain. In Chapter 4, I found that random forest models (RF), optimized for habitat selection analysis, outperformed traditional resource selection functions (RSF) in predicting out-of-sample data and in detecting important features driving sage-grouse habitat selection. My findings suggest that some novel methods may better inform conservation and management, especially when we anticipate important regional variation. They also support the need for wildlife and habitat conservation that is driven by both regional and local environmental conditions to conduct the most effective management.

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APPENDIX

APPENDIX A

CHAPTER 1 SUPPORTING INFORMATION

Table A1. Mean value and standard deviation for every variable in each of the four study areas at every 'available' point used to sample the environment.

Study Area	**Variable**	**Mean**	**SD**
Bald Hills	TPI50	-0.00003	0.3285
Bald Hills	THI50	4.018	5.541
Bald Hills	TPI200	0.004	2.438
Bald Hills	THI200	589.893	673.007
Bald Hills	TPI400	0.0008	5.129
Bald Hills	THI400	4878.595	5258.002
Bald Hills	CAI	4.7844	10.931
Bald Hills	CONTIG	0.1277	0.252
Bald Hills	TREEDIST	593.982	682.662
Bald Hills	TREEDEN400	0.2078	0.1661
Bald Hills	TREEDEN800	0.2079	0.1506
Bald Hills	Slope	4.703	5.307
Cave	TPI50	-0.0014	0.3174
Cave	THI50	3.302	5.4981
Cave	TPI200	-0.0227	2.2879
Cave	THI200	466.939	692.367
Cave	TPI400	-0.0613	4.8788
Cave	THI400	3854.898	5632.998
Cave	CAI	21.763	22.1345
Cave	CONTIG	0.3843	0.3679
Cave	TREEDIST	353.476	428.204
Cave	TREEDEN400	0.093	0.1699
Cave	TREEDEN800	0.0931	0.1642
Cave	Slope	4.092	5.726
Hamlin	TPI50	0.00082	0.2109
Hamlin	THI50	2.6893	3.489
Hamlin	TPI200	-0.0039	1.4598
Hamlin	THI200	351.112	396.724
Hamlin	TPI400	-0.0165	3.0466
Hamlin	THI400	2760.63	3192.937
Hamlin	CAI	13.676	20.559
Hamlin	CONTIG	0.2522	0.3499
Hamlin	TREEDIST	657.693	570.054
Hamlin	TREEDEN400	0.0378	0.1207

Hamlin	TREEDEN800	0.0382	0.1168
Hamlin	Slope	2.63	3.649
Panguitch	TPI50	-0.0013	0.4048
Panguitch	THI50	4.9415	6.8186
Panguitch	TPI200	-0.0114	2.9755
Panguitch	THI200	760.652	773.187
Panguitch	TPI400	-0.0503	6.4435
Panguitch	THI400	6646.89	6082.653
Panguitch	CAI	20.6367	21.5395
Panguitch	CONTIG	0.3678	0.3656
Panguitch	TREEDIST	188.318	438.611
Panguitch	TREEDEN400	0.171	0.236
Panguitch	TREEDEN800	0.171	0.221
Panguitch	Slope	6.608	6.432

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Thesis: Microtopoclimatic effects on a climate-sensitive habitat specialist, the American pika (*Ochotona princeps*)

B.A., Biology-Environmental Studies, Whitman College, Walla Walla, WA (2011)
Advisor: Dr. Tim Parker, parkerth@whitman.edu
Thesis: Factors affecting American pika habitat in North Cascades National Park Service Complex, WA

Experience

Graduate Research Assistant (January 2018-present) & **Research technician** (October 2017-January 2018), Utah State University.

Managed a project studying greater sage-grouse (*Centrocercus urophasianus*) at their southern range margin using GPS transmitters, including live capture and analyzing movement, habitat selection, response to management actions, and impacts of climate. Also assisted in capture and/or handling of coyote, beaver, and mountain lion.

Biological Science Technician (Wildlife), Katmai National Park and Preserve, May 2017-October 2017.

Bear management and monitoring: tracked brown bear behavior and locations while managing the interactions between bears and humans in the park, including direct hazing, habitat use surveys, and data management and analysis.

GIS/Remote Sensing analyst, Denver Zoo Front Range Pika Project; March-April 2017, June-August 2018.

Contracted independently to develop and implement a protocol for mapping potential habitat for pikas in the Front Range and across Colorado.

Contracted to design a statistically rigorous protocol for selecting sties for long term monitoring.

Research Associate, University of Colorado Boulder/Rocky Mountain National Park, May-December 2016.

Awarded research grant as PI to use occupancy surveys and GIS/remotely sensed data to develop a long-term pika monitoring protocol for the Park as indicators of overall ecosystem change.

Graduate Researcher, University of Colorado Boulder/Institute of Arctic and Alpine Research, August 2012-May 2016.

Developed and conducted research projects, including data collection, processing, and analysis; presented results in publication and presentation form; and collaborated with other researchers.

Field crew leader: North Cascades National Park (3x), Yellowstone National Park (2x)

Teaching assistant, General Biology lab (Fall 2012, Spring 2013, Spring 2014), Ecology lab (Fall 2013, Fall 2014, Spring 2014, Fall 2015, Spring 2016).

Biological Technician, Yellowstone Wolf Project, National Park Service, Yellowstone National Park February-August 2012, June 2013.

Tracked wolf behavior and predation by radio telemetry and direct observation. Analyzed role of landscape features in wolf predation on Yellowstone ungulates.

Field Instructor, Teton Science Schools, Jackson, WY, May – August 2011.

Taught field-based science in and around Grand Teton National Park to participants aged 7 to adult.

Volunteer technician, Friends of the Teton River, July-August 2011

Performed habitat assessment of tributary creek around proposed dam site and prepared scientific report and pamphlet for public distribution.

Biological Technician, Beartooth Wildlife Research, North Cascades National Park, May – August 2010.

Conducted field surveys to determine American pika occupancy and habitat characteristics.

Prepared reports culminating in senior thesis for Biology degree—*Factors affecting pika habitat and populations in North Cascades National Park, WA*

Stream habitat intern, Doan Creek restoration project, Whitman Mission NHS, Walla Walla, WA, February-May 2011

Collected, maintained, and analyzed data for the restoration of a creek with mammal, bird, and salmonid populations.

Naturalist, Summer 2008, YWCA Camp Westwind, a residential outdoor camp on the Oregon coast

Designed and ran the camp's nature program, including hikes and ecosystem studies.

Publications

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"Thermal stress drives risky habitat selection in sage-grouse." **Southwest Desert (SWARM) Utah local working group meeting**, virtual, September 7, 2021.

"Thresholds and land cover effects on sage-grouse response to thermal extremes." **Ecological Society of America Annual Meeting**, virtual, August 5, 2021.

"Regional variation in greater sage-grouse response to temperature and use of thermal refugia." **Color Country (CCARM) Utah local working group meeting**, virtual, June 9, 2021.

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"Greater sage-grouse use of thermal refugia on their warm range margin." **Utah Chapter, The Wildlife Society Meeting**, virtual, March 17, 2021.

"Topography and sagebrush contiguity moderate the importance of tree cover on greater sage-grouse habitat selection." **Ecological Society of America Annual Meeting**, virtual, August 5, 2020.

"Nevada greater sage-grouse habitat selection and movements." **Nevada sage-grouse research meeting**, Ely, NV, November 14, 2019.

"Topography and sagebrush contiguity moderate the importance of tree cover on greater sage-grouse habitat selection: Random Forest outperforms mixed effects GLM." **The Wildlife Society Annual Meeting**, Reno, NV, October 1, 2019.

“Habitat selection by greater sage-grouse at their southern range margin.” **Utah All Lands All Hands Meeting**, Salt Lake City, UT, February 7, 2019.

“Developing a protocol for long-term population monitoring and habitat projections for a climate-sensitive sentinel species to track ecosystem change and species range shifts.” **American Geophysical Union Fall Meeting**, San Francisco, CA, December 14, 2016.

“Predicting Territory Occupancy and Microrefugia for a Habitat Specialist, the American Pika (*Ochotona princeps*) Using High Resolution Remotely Sensed Data.” CU EBIO departmental Brown Bag Seminar series, Boulder, CO, March 16, 2016.

“Using High Resolution Remotely Sensed Data to Predict Territory Occupancy and Microrefugia for a Habitat Specialist, the American Pika (*Ochotona princeps*).” **American Geophysical Union Fall Meeting**, San Francisco, CA, December 15, 2015.

“Seasonality in the use of heterogeneous terrain by a territorial habitat specialist.” **Long-Term Ecological Research Network All Scientists Meeting** (poster), Estes Park, CO, August 31, 2015.

“Fine-scale topographic heterogeneity creates suitable microhabitat for a climate sensitive habitat specialist.” **North American Pika Consortium Meeting**, Golden, CO, April 17, 2015.

“Community interactions, trophic cascades, and landscape effects.” CU-Boulder Ecology course guest lecture, Boulder, CO, March 17, 2015.

“Testing territory occupancy hypotheses for a habitat specialist, the American pika.” Guild of Rocky Mountain Ecologists and Evolutionary Biologists conference talk, Pingree Park, CO, September 20, 2014.

“Conservation in wildlife ecology: metapopulation dynamics and pika territory occupancy patterns.” CU-Boulder Conservation Biology course guest lecture, Boulder, CO, June 10, 2014.

“Conservation in wildlife ecology: landscape effects on trophic cascades and wolf predation.” CU-Boulder Conservation Biology course guest lecture, Boulder, CO, June 6, 2014.

“Seasonal patterns of wolf predation in Yellowstone.” Whitman College geology and environmental studies field trip to Yellowstone National Park, May 28, 2012.

“Wolf behavior and population dynamics in Yellowstone.” Teton Science Schools graduate student tour of Yellowstone National Park, April 25, 2012.

Funding: total awarded=$40,002

Received Utah State University Ecology Center gradate research grant ($5,000), March 2020.
Received Rocky Mountain National Park research grant ($11,313), February 2016.
Received David Paddon Memorial Grant, Indian Peaks Wilderness Alliance ($600), May 2015.
Received CU-Boulder Department of Ecology and Evolutionary Biology departmental research grant ($2,409), April 2015.
Received Yellowstone Park Foundation research grant ($7,980), May 2014.
Received Joyce Gellhorn Memorial Grant, Indian Peaks Wilderness Alliance ($1,000), May 2014.
Received CU-Boulder Department of Ecology and Evolutionary Biology departmental research grant ($2,100), May 2014.
Received CU-Boulder Department of Ecology and Evolutionary Biology departmental research grant ($2,000), April 2013.
Received David Paddon Memorial Grant, Indian Peaks Wilderness Alliance ($500), May 2013.

Skills

Programming and computation

- **R:** Spatial data processing, statistical analyses, machine learning, data management, species distribution modeling, topographic analysis, remote sensing data processing, habitat selection, Bayesian statistics
- **ArcGIS:** Data processing, model building, data management, cartography, remote sensing data processing, spatial statistics, interpolation
- **ENVI:** Remote sensing data processing, land cover mapping
- **Python:** Spatial data processing and management

Field skills

- **Live capture and handling:** Assisted and/or led handling of sensitive species including greater sage-grouse, American pika, and beaver.
- **Backcountry travel and navigation:** Extensive experience navigating and covering rough terrain in inclement weather using GPS or topographic maps.
- **Population surveys:** Sight-resight, minimum population counts, point counts, line transect counts.
- **Vehicles:** Experienced and comfortable traveling by 4x4 and ATV and hauling a trailer.
- **Firearms:** Shotgun certified by National Park Service.
- **Other:** Field and lab necropsies, vegetation surveys