Habitat Specialists as Conservation Umbrellas:
Do Areas Managed for Greater Sage-grouse Protect Pygmy Rabbits?

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Authorization to Submit Thesis

This thesis of Ian T. Smith, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Habitat Specialists as Conservation Umbrellas: Do Areas Managed for Greater Sage-grouse also Protect Pygmy Rabbits?," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Sagebrush ecosystems are affected by a variety of factors, and loss and degradation of sagebrush habitat threatens many wildlife species. Federal land management and wildlife agencies have invoked the umbrella species concept to protect this ecosystem, designating >580,000 km^2 as Habitat Management Areas (HMAs) for greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") putatively benefiting multiple wildlife species. The pygmy rabbit (*Brachylagus idahoensis*) also is a species of conservation concern due to its obligate relationship with the sagebrush ecosystem, and our goal was to evaluate the degree to which sage-grouse-focused HMAs and distribution might serve as a conservation umbrella for pygmy rabbit habitat. We used maximum entropy methods to build species distribution models of varying complexity at two scales: 1) across the geographic range of pygmy rabbits, and 2) focusing on a regional extent in east-central Idaho that also included seasonal variation in distribution of sage-grouse. Across the geographic range, our results indicated that Priority HMAs encompassed 59% and General HMAs encompassed of 34% of primary habitat for pygmy rabbits. At the regional extent, we found moderate degrees of spatial overlap between these species across space (50% of pygmy rabbit habitat within sage-grouse habitat) but less overlap when we evaluated specific seasonal models of sage-grouse distribution (18-31% of pygmy rabbit habitat in a given seasonal habitat for sage-grouse). Our models predicted that pygmy rabbits may occur in thin sagebrush corridors (e.g., 1 km width) between steep terrain features where sage-grouse often are absent. Our sage-grouse models represent a rich location dataset that can provide useful information to researchers and land managers alike. The species distribution models defining habitat for pygmy rabbits can be used by land managers and biologists to prioritize survey locations for pygmy rabbits and to identify areas for habitat management, conservation, or restoration at range-wide and regional extents.

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Dedication

To my parents, Kristen and Bruce, for their unwavering support.

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General Introduction

The world's natural places and wildlife populations have been increasingly fragmented and impacted by anthropogenic activities, resulting in ecosystem degradation and biodiversity loss. Limited resources available for wildlife and habitat conservation have led to the development and application of simplified strategies for achieving conservation objectives. Additionally, identifying the correct scale(s) for data analysis and application of research results to management is complicated when studies conducted at different temporal and spatial scales lead to conflicting conclusions and conservation recommendations (Wiens 1989, Levin 1992). Investigations conducted at multiple spatial and temporal scales or across scale gradients can be useful in informing land management and conservation decisions (e.g., Schwartz 1999, Ricklefs 1987, Rahbek 2005, Hurlbert and Jetz 2007). This is especially true when conservation strategies conceptually appropriate for broad extents are assumed to provide useful information for conservation actions at fine spatiotemporal scales.

Surrogate species strategies, such as the conservation of umbrella species, attempt to simplify the concerns and goals of what can be a wide range of habitats and species into a more unified set. The umbrella species concept is used to identify a species that requires relatively large areas and encompasses the resource needs of sympatric species under a targeted set of rules and regulations (Caro and O'Doherty 1999, Caro 2003, Roberge and Angelstam 2004). Evaluation of this strategy and other surrogate species approaches have yielded mixed results leading to skepticism regarding their efficacy (Andelman and Fagan 2000, Fleishman et al. 2000, Branton and Richardson 2011). Additionally, these strategies often are not evaluated across a range of scales.

We chose a high-profile umbrella species, the greater sage-grouse (*Centrocercus urophasianus*), and another sagebrush obligate species, the pygmy rabbit (*Brachylagus idahoensis*), to investigate the efficacy of the umbrella species concept and species overlap at two scales: 1) across the geographic range of pygmy rabbits and 2) within a regional landscape in east-central Idaho where both species co-occur. These two species are unique among vertebrates in being tightly coupled to sagebrush steppe ecosystems in the western US. Concern over these ecosystems prompted conservation and management of sagebrush steppe landscapes in the name of sage-grouse and has resulted in the largest scale conservation effort in US history (Goldfuss et al. 2015). The main units of land conserved using this strategy are called sage-grouse Habitat Management Units (HMAs). Although it is assumed that conservation aimed at enhancing sage-grouse persistence benefits other sagebrush associated species, like the pygmy rabbit, relatively little quantitative evidence of this exists (but see Rowland et al 2006, Hanser and Knick 2011, Carlisle et al. 2018).

Our goal was to evaluate how well habitat management plans for sage-grouse encapsulate pygmy rabbit habitat at the geographic range scale, and to quantify species overlap at finer spatiotemporal scales that are amenable to habitat management. To do this, we used species distribution modeling (SDM) to map habitat for pygmy rabbits at the geographic range scale, producing the first geographic range map of this kind for the species. We compared this distribution to the estimated sage-grouse distribution and to sage-grouse HMAs across the range of pygmy rabbits. Within our regional assessment area, we built SDMs for pygmy rabbits and for three different seasonal habitats for sage-grouse. These methods allowed us to investigate species overlap across both spatial and temporal scales. Our models and analyses of overlap between species can serve as conservation tools for land managers seeking to accomplish habitat protection for these sagebrush obligates. Our study also provides an evaluation of the umbrella species approach for two highly specialized species that share a major resource requirement, the presence of sagebrush. We provide an assessment that exemplifies how generalizations regarding species habitat associations may be less applicable as spatiotemporal scales decrease. Our results have implications for the persistence of species of concern under simplified conservation strategies.

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Chapter 1: Habitat Specialists as Conservation Umbrellas: Do Areas Managed for Greater Sage-grouse Protect Pygmy Rabbits

(submitted to *Ecosphere*, coauthors: Janet L. Rachlow, Leona K. Svancara1, Laura A.
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Abstract

Sagebrush ecosystems are affected by a variety of factors and loss of sagebrush habitat threatens many wildlife species. Federal land management and wildlife agencies have invoked the umbrella species concept to protect this ecosystem, designating >580,000 km^2 as Habitat Management Areas (HMAs) for greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") putatively benefiting multiple wildlife species. The pygmy rabbit (*Brachylagus idahoensis*) also is a species of conservation concern due to its obligate relationship with the sagebrush ecosystem. Our goal was to evaluate the degree to which grouse-focused HMAs might serve as a conservation umbrella for pygmy rabbit habitat. We acquired 18,598 records of pygmy rabbit occurrence from all eight range states (excluding Washington because that population is undergoing reintroduction); after screening for reliability, we retained 10,420 records, which we used to estimate minimum occupied area (MOA) and to create a species distribution model (SDM) for pygmy rabbits across their full geographic range. We used the program Maxent to build models of varying complexity, incorporating topographic, vegetation, fire, climate, and soil information. The pygmy rabbit MOA is estimated at 28,089 km^2, and ~92% of this area is included within HMAs. We identified 224,820 km^2 of suitable habitat for pygmy rabbits (maximum test sensitivity plus specificity threshold of 0.3167) and 145,725 km^2 of primary habitat (equal test sensitivity and specificity threshold 0.4661), with concentrations in four distinct core areas. Overlap with sage-grouse HMAs was high (87% of suitable habitat and 91% of primary habitat), suggesting that the sage-grouse umbrella has the potential to conserve habitat for pygmy rabbits. Two of the largest HMAs are Priority Habitat Management Areas (PHMAs; which have the most habitat protection) and General Habitat Management Areas (GHMAs; which have less protection). Our results suggest that PHMAs encompass 59% and GHMAs encompass of 34% of primary habitat for pygmy rabbits. The SDM of habitat for pygmy rabbits can be used by

land managers and biologists to prioritize survey locations for pygmy rabbits and to identify areas for habitat management, conservation, or restoration.

Introduction

Surrogate species strategies often are employed as streamlined approaches to address conservation objectives. The umbrella species concept is one such strategy used to protect biodiversity and conserve habitats or ecosystems (Caro and O'Doherty 1999). Umbrella species are commonly used to identify regions for focused conservation attention, thereby protecting sympatric species by encompassing their resource needs under a targeted set of rules and regulations without special consideration of each sympatric species (Caro 2003, Roberge and Angelstam 2004). Assessments of applications of umbrella and other surrogate species approaches have yielded mixed results leading to skepticism regarding the efficacy of these conservation strategies (Andelman and Fagan 2000, Fleishman et al. 2000, Branton and Richardson 2011, Carlisle et al. 2018).

Conservation of sagebrush ecosystems in the western USA is primarily addressed through protection of habitat for a high-profile species of conservation concern, the Greater sage-grouse (*Centrocercus urophasianus*), hereafter referred to as sage-grouse. These relatively large, charismatic game birds are obligate to sagebrush communities and well-known for elaborate mating displays conducted on traditional lekking grounds (Johnson and Rowland 2007, Knick and Connelly 2011). Sage-grouse now occupy an area of about 67 million ha range-wide, about half of their estimated range before European settlement (Connelly et al. 2004). Although populations exhibit cyclic patterns, long-term sage-grouse numbers are estimated to be in decline by separate modeling efforts and updated datasets (Connelly et al. 2004, Crawford et al. 2004, Garton et al. 2015, Edmunds et al. 2018). One study estimated that the minimum number of breeding males range-wide fell by 56% between 2007 and 2013 (Garton et al. 2015). Because they are sagebrush obligates that use relatively large areas (i.e., a "landscape species"), sage-grouse have long been considered an umbrella species for conservation of the sagebrush ecosystem (Rowland et al. 2006, Connelly et al. 2011). In fact, concern about the well-being of sage-grouse populations and potential listing under the Endangered Species Act (ESA) launched "the largest landscape-level conservation effort in US history" (Goldfuss et al. 2015).

The sagebrush ecosystem is the largest semi-arid shrub community in North America, and it is simultaneously one of the most imperiled and neglected ecosystems (Dobkin and Sauder 2004, Homer et al. 2015). Sagebrush occurs in large portions of 11 western states and once occurred on >150 million ha (Anderson and Inouye 2001, Dobkin and Sauder 2004, Wisdom et al. 2005). Today, the sagebrush biome has been reduced to 40-50% of its pre-European settlement area, now encompassing an estimated 62-100 million ha, less than 10% of which is relatively undisturbed by human activities (West 1983, Connelly et al. 2004, Wisdom et al. 2005). Declining quality and quantity of sagebrush habitat has been linked to numerous interrelated factors and detrimental feedback loops (Anderson and Inouye 2001, Miller and Eddleman 2001, Bunting et al. 2002, Knick et al. 2003). Invasion of non-native plants, primarily cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*), encroachment of conifers such as juniper (*Juniperus* spp.) and pinyon pine (*Pinus momphylla*) and changing fire regimes can impact sagebrush stands and threaten sagebrush communities. These vegetative state changes are exacerbated by shifting anthropogenic land uses and climate change (Bradley 2010, Schlaepfer 2012, Palmquist 2016). Human activities such as livestock grazing, energy production, urban and ex-urban development, fire control, and expanding agriculture all play a role in the depletion and fragmentation of this ecosystem.

The loss and alteration of sagebrush ecosystems has had negative impacts on diverse taxa (Wisdom et al 2000, Rowland et al. 2010; 2011). Analyses of trends across the sagebrush biome have cautioned that many sagebrush-dependent species are not currently found in areas reflected by standard range maps (Dobkin and Sauder 2004). Over 630 species of plants and animals are associated with sagebrush systems, and >60 bird and small mammal species depend extensively on the system (Dobkin and Sauder 2004, Suring et al. 2005, Rich et al. 2005, Wisdom et al. 2005), and many of these species are either in decline or of unknown population status with declines suspected (Wisdom et al. 2005, Rowland et al. 2011).

Nearly 70% of the existing sagebrush habitats in the western USA occur on public lands, and all 11 states where sage-grouse occur have developed strategic management plans for the species (Connelly et al. 2004, Stiver 2011). These coordinated plans constitute a sage-grouse umbrella that designates >580,000 km^2 as sage-grouse Habitat Management Areas

(HMAs) (BLM 2015). Sage-grouse HMAs are land units managed by the Bureau of Land Management (BLM) and US Forest Service (USFS) in cooperation with the US Fish and Wildlife Service (USFWS) to preserve sagebrush habitats to varying degrees for the benefit of sage-grouse. HMAs do not represent habitat protection as it is traditionally accomplished (i.e., through designation of national parks, wilderness, wildlife refuges, etc.), but instead HMAs are areas identified as being important habitat for sage-grouse, and therefore, management of these areas involves consideration of sage-grouse to some degree (BLM 2015). HMAs are currently being revised and will likely always be in a state of flux.

There are five types of HMAs: Priority, Important, General, Other, and Linkage Connectivity. Priority HMAs (PHMAs) are distributed throughout sage-grouse range, have the highest habitat value for sustaining sage-grouse populations, and incorporate all seasonal habitats. Within PHMAs, surface disturbance is avoided or minimized to the greatest extent relative to other HMA types. Important HMAs (IHMAs) are designated only in Idaho and typically represent lower quality sage-grouse habitat adjacent to and connecting patches of PHMAs. General HMAs (GHMAs) are distributed throughout the sage-grouse range in areas outside of PHMAs, and largely represent areas of lower habitat quality, either because they are occupied only seasonally or because they are in areas of lower connectivity. Other HMAs (OHMAs) occur only in Nevada and California and sometimes serve as buffers for PHMAs or connect PHMA patches (BLM 2015). Linkage Connectivity HMAs (LCHMAs) are designated only in Colorado and represent important regions to facilitate sage-grouse movement between PHMAs and GHMAs in Colorado (BLM 2017). A relatively small (16,673 ha) area of Anthro Mountain, in Utah is designated separate from HMAs but managed for continued sage-grouse survival while allowing natural gas mining and development. The spatial extent of HMAs was updated in October 2017 with revisions in Wyoming and an Approved Resource Management Plan Amendment (BLM 2017).

An understanding of overlap between sage-grouse HMAs and other sagebrush-dependent wildlife is critical for moving from single-species conservation to comprehensive strategies that maintain ecosystem function and support biodiversity in sagebrush landscapes. The value of a sage-grouse umbrella is likely influenced by similarities between this bird and other target species with respect to taxonomic affiliations, body size, trophic level, and resource requirements. Hanser and Knick (2011) concluded that sage-grouse might be an effective umbrella species for most sagebrush-associated wildlife, although somewhat more reliable for passerine birds than small mammals. Furthermore, the total area of habitat conserved could be more important than specific habitat characteristics or locations (Carlisle et al. 2018).

Like sage-grouse, the pygmy rabbit (*Brachylagus idahoensis*) is considered a sagebrush obligate. Pygmy rabbits are currently designated as a species of greatest conservation need or a species of concern in all 9 range states (including Washington), although some states have not yet developed conservation plans for the species (USGS 2018a). The Columbia Basin pygmy rabbit in Washington, USA, was federally listed as an endangered distinct population segment in 2003 (Federal Register 2003), and the species was petitioned for range-wide protection under the ESA in the same year. In 2010, the USFWS concluded that ESA listing was not warranted for the entire species, in part because the species still occurred across the breadth of its historic geographic range (Federal Register 2010). Although pygmy rabbit populations occur across this range, their distribution is highly patchy, and a map of species distribution within the boundaries of the geographic range is not available. In addition to quantifying the pattern of occurrence, an accurate map of the distribution of potential habitat is needed to assess the conservation status of pygmy rabbits, to evaluate regional patterns of occupancy and habitat relationships, and to quantify changes in distribution over time. Additionally, given the conservation focus on habitat for sage-grouse, an evaluation of potential overlap between the two species across their ranges can help land managers plan for conservation of multiple species of concern, especially those that are tightly coupled with the sagebrush ecosystem.

Although sage-grouse and pygmy rabbits are both sagebrush obligates, their resource needs likely differ at least during some periods of the annual cycle. Two general habitat features are associated with the year-round presence of pygmy rabbits: (1) relatively dense and tall sagebrush vegetation; and (2) soil characteristics that are conducive to burrowing, such as the presence of deep, loamy soils, and features such as alluvial fans and mima mounds (Borell and Ellis 1934, Weiss and Verts 1984, McMahon et al. 2017). Unlike pygmy rabbits, sage-grouse shift habitat use across the year, and biologists often consider spring breeding, summer brood rearing, and winter habitats as distinct (Fedy et al 2014, Rice et al 2016).

Our goal was to evaluate how habitat conservation strategies designed for sage-grouse might perform for pygmy rabbits. We synthesized existing range-wide information on occurrence of pygmy rabbits and created the first comprehensive geospatial dataset and occurrence map. Our assessment did not include Washington because populations there are a result of on-going reintroduction efforts following extirpation (Becker et al. 2011, DeMay et al. 2017). We used the data on occurrences to build an inductive species distribution model (SDM) using maximum entropy (Maxent; Phillips et al. 2004; 2006, Phillips and Dudík 2008). We estimated the minimum occupied area (MOA) for pygmy rabbits using trusted observations and home range information. We then quantified overlap by comparing our SDM and estimate of MOA to the estimated current distribution of sage-grouse, complied by Schroeder et al. 2004, and to the sage-grouse HMAs. We hypothesized that habitat modeled as suitable for pygmy rabbits would reflect the current understanding of resource requirements and habitat selection for this species. We expected that suitable habitat would be strongly associated with sagebrush shrub cover, relatively tall shrub heights, and deep soils (i.e., >25cm to restrictive layer). Pygmy rabbit distribution has been described as patchy or disjunct across a diversity of scales (Weis and Verts 1984, Estes-Zumpf et al. 2010), and we expected this trend to be apparent at the range-wide scale both in distribution of MOA and habitat modeled as suitable. We also hypothesized that designated land management areas for sage-grouse would encompass most of the known pygmy rabbit occurrences and predicted suitable habitat throughout their range due to the close association with sagebrush exhibited by the two species. We expected that PHMAs would incorporate habitat for pygmy rabbits to a greater extent than GHMAs because PHMAs encompass higher quality sagebrush habitats that support sage-grouse across all seasons. We predicted that a greater proportion of pygmy rabbit habitat would be encompassed by PHMAs than GHMAs. Like many conservation heuristics, the umbrella species concept is often untested with empirical evidence. Quantifying the degree to which the sage-grouse umbrella is conserving other sagebrush obligates is important for biodiversity, land management, and for the sustainability of wildlife of concern like the pygmy rabbit.

Methods

Study Area

Our study encompassed an expanse of the western USA that included large parts of Nevada, Utah, Wyoming, Oregon, and Idaho as well as relatively small portions of California, Montana, and Colorado (Fig. 1a). This area included lands in the Great Basin, Wyoming Basin, Columbia Plateau, and Colorado Plateau Ecoregions. We defined the full extent of the modeling area using the species range for pygmy rabbits (excluding the disjunct reintroduced population in Washington) identified in the Gap Analysis Project (GAP) buffered by 100km (USGS 2018b). This area (1,217,622 km^2) encompassed all pygmy rabbit occurrence points. We also used state boundaries and Bailey's Ecological Subregions, also known as Ecological Sections (Bailey 2016), to reference specific regions within the study area.

Pygmy rabbit occurrence

We compiled a comprehensive dataset on occurrence of pygmy rabbits across their range. Data were provided by state wildlife agencies, natural heritage programs, and individual biologists. A total of 18,598 records were obtained from Nevada (2,498), Utah (727), Wyoming (8,589), Oregon (660), California (12), Idaho (4,894), Montana (1,213), and Colorado (5). We first screened the location data to retain only high-quality records using three rules (Phillips and Dudík 2008, Aubry et al. 2017): [1] Reliability—Any records categorized as "questionable", "uncertain", or a synonymous term were excluded from model consideration whereas records with a "trusted" or "verified" label were retained; [2] Time Period—We excluded 767 of the records that were collected before 2000 to build a model that reflected the recent distribution of the species; and [3] Spatial Accuracy—We excluded records with a locational uncertainty or error >250 m to screen for spatial accuracy using a biologically relevant distance (i.e., approximate diameter of an adult female home range, Estes-Zumpf and Rachlow 2009).

Of remaining records, incidental or anecdotal observations were separated from observations acquired during field surveys. Incidental records were subject to higher scrutiny than records from surveys because we assumed that data collected during field surveys would have a higher level of identification accuracy due to observer training. When it was not possible to distinguish between an anecdotal (general or incidental) observation and an observation collected as part of a survey, the record was considered anecdotal. Records deemed anecdotal were scanned for keywords describing three types of pygmy rabbit sign: (1) rabbit pellets (scat or droppings); (2) pygmy rabbit burrows (also recorded as entrances, diggings, holes, etc.); or (3) a visual observation. Records were retained if they referenced at least two of these signs or other clear evidence such as live capture, collection of a specimen or DNA, photographs, or record of a telemetry location. Records from surveys by land or wildlife management agencies (e.g., BLM, USFS, or USFWS) or other professional groups were retained when there was a description of observation, activity, or sign. These screening measures reduced our pygmy rabbit occurrence list to 10,420 trusted location records.

To minimize sampling bias, we partially reduced the spatial autocorrelation of the occurrence data by spatially filtering, or subsampling, the trusted location dataset as recommended for best modeling practices (Phillips et al. 2009, Kramer-Schadt et al. 2013, Radosavljevic and Anderson 2014). Acquired presence data were likely biased as some regions had been surveyed more intensely than others across the range (e.g., southwestern Wyoming, east-central Idaho, and southwestern Montana). We spatially subsampled the trusted locations using a minimum distance of 800 m, which matched the coarsest resolution environmental data (climate data). This step resulted in a total of 1,809 occurrence locations available for model training and testing.

We used the all trusted location records (n = 10,420) to create a map of the recent, known distribution of pygmy rabbits to estimate the minimum geographic area occupied (MOA). We buffered each trusted location by 3km, which is approximately equal to the median natal dispersal distance documented for the species (Estes-Zumpf and Rachlow 2009, Estes-Zumpf et al. 2010) and also close to one estimate of the width of an average female home range (Sanchez and Rachlow 2008). We then erased areas known to be non-habitat for the species (i.e., areas mapped as urban and developed or open water [USGS GAP 2016] and used this information to estimate MOA.

Environmental variables

We developed environmental variables that represented abiotic and biotic factors likely related to occupancy by pygmy rabbits. Environmental data were acquired from multiple sources, projected into a common coordinate system (NAD 1983 Albers), and resampled to 30 m resolution, as needed (Appendix A). Land cover types that were considered non-habitat (i.e., urban and developed or open water) were not evaluated as environmental predictor variables, but instead were excluded from possible background consideration and map prediction. We did not exclude agricultural lands, however, because pygmy rabbit locations sometimes occurred in areas mapped as agriculture, and although pygmy rabbits generally avoid cultivated fields, they can use areas close to fields (e.g., shrub rows along fences).

Topographic features that promote soil deposition are common in areas occupied by pygmy rabbits and likely characterize areas inhabited by the species. We evaluated four measures of topographical variation: elevation, aspect, slope, and curvature using USGS Digital Elevation Models (USGS 2016). Our curvature layer was created using the curvature tool in ArcGIS 10.3.1 (ESRI 2016). Although not always identified as important indicators of habitat quality, topography impacts biological processes and these measurements (i.e., elevation, slope, aspect, and curvature) are sometimes included as environmental variables in predictive models, partly because they are more accurate than interpolated bioclimatic variables (Guisan and Zimmermann 2000, Lassueur et al. 2006).

Because pygmy rabbits are obligate burrowers (Green and Flinders 1980), we included soil parameters that might influence suitability of sites for burrow excavation. Pygmy rabbits often are associated with loamy, friable soils that are favorable for digging, and indeed, the heterogeneous distribution of these soils potentially contributes to the patchy distribution of the species (Weiss and Verts 1984). Deep and loamy soils not only facilitate burrowing, but they also tend to support relatively dense and tall sagebrush stands (Winward 1980, Davies et al. 2011), which are used by pygmy rabbits. We downloaded data from the POLARIS database, which contains a high resolution, probabilistic soil map of the USA created using a machine learning algorithm that remapped the Soil Survey Geographic Database (SSURGO; Chaney et al. 2016). We estimated mean values of six soil characteristics (bulk density, calcium carbonate percentage, clay percentage, sand percentage, silt percentage, and pore size distribution) by averaging all depth bins within 1 m. We also evaluated data on depth to the restrictive layer, which was a single value and therefore not averaged.

Previous studies have identified vegetation type, shrub canopy cover, herbaceous cover, and shrub height to influence habitat selection by pygmy rabbits. For example, big sagebrush (*Artemisia tridentata* spp.) comprised up to 99% of pygmy rabbit winter diets and about 50% of summer diets (Shipley et al. 2006), and pygmy rabbits occurred at sites with relatively dense and tall sagebrush vegetation (Katzner and Parker 1997, Lee et al. 2010, McMahon et al. 2017). To that end, we selected variables that measured the extent of big sagebrush communities, the majority shrub canopy cover, majority percent herbaceous cover, and the maximum and majority shrub height within a 90 m neighborhood (3x3 cell). This neighborhood scale is aligned with the size of an individual's home range (Crawford et al. 2004, Rachlow et al. 2005; Sanchez and Rachlow 2008, Camp et al. 2012; Lee et al. 2010). For big sagebrush, we selected 6 ecological systems from GAP/Landfire National Terrestrial Ecosystems dataset (USGS GAP 2016): inter-mountain basins mixed salt desert scrub, Great Basin xeric mixed sagebrush shrubland, inter-mountain basins big sagebrush shrubland, inter-mountain basins big sagebrush steppe, inter-mountain basins montane sagebrush steppe, Wyoming basin dwarf sagebrush shrubland and steppe. These systems had at least two big sagebrush associations listed in Natureserve (2018).

We used LANDFIRE Existing Vegetation Cover (Landfire 2016) to characterize shrub canopy cover and herbaceous cover. Raster values reflect a range of cover estimates within 10% bins. We reclassified this range to the bin median value (e.g., grid cells of 30-40% shrub cover were assigned a value of 35%) and then calculated the majority value within a 90 m neighborhood. Similarly, we reclassified LANDFIRE Existing Shrub Height to median values for each cell (e.g., grid cells 50–100cm shrub height were assigned a value of 75cm) and then used a 90 m neighborhood to calculate both a maximum and majority shrub height value for each cell, resulting in two variables, shrub height majority and shrub height maximum. The average Normalized Difference Vegetation Index (NDVI) layer was obtained through the USGS eMODIS remote sensing phenology data to represent the average canopy photosynthetic activity across the entire growing season from 2001 to 2015 (USGS 2018c).

An understanding of how climate influences the distribution of pygmy rabbits is not well-developed, however, they live in strongly seasonal environments. Additionally, increased precipitation seasonality coupled with longer dryer summers are predicted by current climate modeling which can negatively impact sagebrush communities (Schlaepfer 2012, Palmquist 2016). Using monthly temperature and precipitation normals (i.e., long-term datasets describing average conditions from 1981-2010) from the Parameterized Regression on Independent Slopes Model (PRISM, Version 14.1-20140502-1000; PRISM 2012, Daly et al.

2015), we calculated 19 bioclimatic variables patterned after Hijmans et al. (2005). These variables have been used extensively in species distribution modeling and wildlife habitat modeling (e.g., Elith et al. 2006, Anderson and Gonzalez 2011, Stanton et al. 2012) to capture the climactic envelope within which species persist.

Stand replacing fires in sagebrush communities can alter and eliminate habitat for pygmy rabbits. We evaluated two parameters describing fire characteristics sourced from the Landfire Historical Fire Frequency and Severity data (Landfire 2016). The Mean Fire Return Interval provides ordinal ranges of mean fire return intervals in years, and we reclassified it so that each raster cell was assigned a value corresponding to the median of that interval (e.g., a fire interval of 11-15 years was given a new value of 13). We considered this reclassification to be a reasonable method for our purposes because resulting response curves would be based on neither a maximum nor minimum fire interval, but on values closer to the median expected return time. We then calculated the majority of a 90 m window around each grid cell to smooth the layer. When the calculation returned a value of ‘No Data’ because there was no majority within the neighborhood, the cell value was reassigned the original median value. This same process was repeated for the Fire Regime layer, a characterization of historical fire regimes based on vegetation and fire dynamics including fire return interval and fire severity, except that fire regime group values were retained and not changed to a median value.

Species distribution modeling

We used the subsampled trusted occurrence locations and environmental variables to create an inductive model of the distribution of habitat for pygmy rabbits using maximum entropy methods (Maxent 3.4.0; Phillips et al. 2004; 2006, Phillips and Dudík 2008, Phillips et al 2017). Maxent characterizes conditions at occurrence sites, compares that covariate space to those available across the modeled region, and generates an output that measures the degree of similarity to occupied sites. The cloglog output specifically estimates the probability of species presence. We used a modeling approach that reduced autocorrelation in the presence data, explored different background location extents, reduced model complexity, and dealt with degree of model fit by tuning regularization multipliers (Anderson and Gonzalez 2011, Elith et al. 2011, Merow et al. 2013, Radosavljevic and Anderson 2014, Searcy and Shaffer 2016). We accepted the program default setting of all feature types, ran all environmental covariates as continuous variables, and selected the raw output type to calculate performance metrics. We specified the algorithm use 80% of the occurrence locations for model training (the first phase in which the model compares occurrence and background points) and the remaining locations for model testing, when measures of performance such as omission rates and area under the receiver operating characteristic curve (AUC) are generated. We specified cross-validation to estimate the model's predictive performance across 5 replicates.

Choice of a background size has been shown to influence model predictions and experimenting with background size is recommended for best modeling practice (Phillips and Dudík 2008, Phillips et al. 2009, VanDerWal et al. 2009, Merow et al. 2013). We manipulated the background data by sampling background locations from three different background extents. The largest extent was defined by our study area; we call this the "range buffer" extent (this extent is equal to our study area). For the smallest extent, we used a 10 km buffer around the filtered locations, representing an approximate maximum dispersal distance by pygmy rabbits (Estes-Zumpf and Rachlow 2009); we call this the "10 km buffer" extent. The third extent was created with a 50 km buffer around filtered locations representing an intermediate extent; the "50 km buffer" extent. Within each of these extents, we randomly sampled 10,000 background locations separated by a minimum distance of 800 m and outside of unsuitable areas (i.e., not urban, developed, or open water), which served as points of comparison to pygmy rabbit presence locations. Given our large modeling extents and relatively fine cell resolution (30 m), we considered using more than 10,000 background points. However, exploratory analysis of multiple 10,000 and 50,000 background samples demonstrated that the same level of environmental variation was captured with samples of 10,000.

We initially built "full" models with the full set of variables (*n* = 39; Appendix A) at each modeling extent (10 km, 50 km, and range buffer) before reducing variable structure in two ways. First, when two or more variables were highly correlated (Pearson's correlation $\geq$0.7), the variable(s) with lower percent contribution, as calculated by Maxent, were eliminated from model consideration. Second, variables with <2% permutation importance were also iteratively removed. Using this process, we attempted to reduce model complexity at all extents and evaluate if certain modeling extents were associated with different environmental variables. We reduced variables until models at each extent had no highly correlated variables, and all variables gained at least 2% contribution or permutation importance. We call these models with the reduced number of environmental variables “reduced models”.

After the variable reduction process, we explored the effect of different regularization multipliers on model predictions. Increasing regularization reduces the overfitting of models and can help overcome issues of sampling bias and spatial autocorrelation in the presence data (Elith et al. 2011, Warren and Seifert 2011). For each of the models with the reduced variable structure, we ran the model with regularization multipliers of 1, 5, and 10 to evaluate how this wide range of regularization affected output (Radosavljevic and Anderson 2014).

Model evaluation

We evaluated the models using multiple metrics to balance strengths and weaknesses in selecting a final model. Some default outputs of Maxent include a receiver operating characteristic (ROC) area under the curve (AUC) for both testing and training data, omission rates, a binomial test of significance for testing and training data at 11 threshold values, and jackknife evaluations of model gain for all variables. We also calculated the difference between model training and testing AUC. Models usually perform better on training data than testing data, and smaller differences between these AUCs reflect a lower probability of over-parameterization or over-fitting the model (Warren and Seifert 2011).

In addition, we calculated AIC using ENMtools (Warren et al. 2009) to inform model selection, but we did not use AIC to compare models of differing background extents, because each extent used different background locations. Instead, AIC values were compared for models with both the full variable structure and reduced variable structure and different regularization multipliers within each extent (i.e., models of differing complexity and degree of fit to training data; Merow et al. 2013).

Finally, we evaluated model performance and fit using threshold-dependent binomial tests. We examined the 11 different threshold values for which Maxent calculates binomial probabilities based on omission and predicted area. At each of these thresholds, a binary prediction of suitable vs. unsuitable habitat is used to test a null hypothesis that test locations are not predicted with any more certainty than a random prediction, resulting in 11 one-sided *p*-values (Phillips et al. 2006, Radosavljevic and Anderson 2014). We examined these *p*-values across 10 model replicates and used $\alpha = 0.05$ to determine the significance of each test.

Omission rates higher than expected values under an ideal model were uncommon for all thresholds. Together, these metrics, as well as a visual inspection of resulting SDM maps, guided model evaluation and selection.

We produced a species distribution map for pygmy rabbits at the range-wide scale and then classified our study area into three habitat classes using two threshold values. We ran our final model in cloglog format, which produced a predictive map with grid values ranging from 0 to 1. Outputs on this scale can be interpreted as a likelihood percentage that the species will be present in the grid cell. The threshold for unsuitable vs. suitable habitat was the value that maximized the sum of testing sensitivity and specificity (maxSSS: 0.313). This thresholding method is recommended as a binomial classifier for presence-only SDMs because it tends to be more consistent when the occurrence location to background point ratio changes (Liu et al. 2005). The value we used to divide suitable and primary habitat is a value that equalizes test sensitivity and specificity (equalSS: 0.4341). This choice made the most sense given that we used a threshold based on testing data for the first cutoff (i.e., maxSSS) and the equalSS value was one of the only threshold options Maxent calculated that was markedly lower than maxSSS, a desirable outcome for classifying a higher or more suitable habitat level.

We considered the functional sage-grouse umbrella to be lands designated as sage-grouse HMAs. Based on October 2017 spatial data (BLM 2017), 587,298 km^2 of land is designated as HMA, some of which occurs outside of the pygmy rabbit geographic range in Montana, North Dakota, and South Dakota. Within our study area, there are 407,366 km^2 of HMA. The largest HMA types, GHMAs and PHMAs, both cover >150,000 km^2 and occur in all states, while other HMA types are specific to certain states and are generally smaller (Table 1). We estimated umbrella efficacy by calculating overlap ratios of pygmy rabbit distribution (i.e., MOA or modeled suitable and primary habitat) within each of the HMA types that fall within the geographic range of pygmy rabbits (Fig. 1a, Table 1).

Results

Species occurrence

We identified 10,420 trusted records for pygmy rabbits, which constitutes a comprehensive dataset of recent occurrence at the full extent of the species geographic range, excluding the reintroduced populations in the Columbia Basin, Washington. These records are locations where pygmy rabbits have been documented since 2000, and they can serve as a baseline for assessing the MOA. Although our screening process generally did not remove all occurrence records from a given area, many records in the Snake River Plain, Idaho, and the area north of Great Salt Lake, Utah, were collected prior to 2000 and consequently, removed from our analysis. We estimated that the MOA was 28,089 km^2, assuming a 3 km buffer around point locations (Fig. 1b).

The known occurrences of pygmy rabbits reflect a highly patchy distribution throughout their range, as we expected (Fig. 1b). The largest contiguous patches of occurrence are in the Wyoming Basin, but we also identified relatively large patches in east-central Idaho and southeastern Montana, in southwestern Idaho, and near the intersection of the Oregon, Nevada, and California borders. The states with the greatest estimated occupied areas are Wyoming (8,517 km^2), Idaho (7,692 km^2), and Nevada (6,374 km^2), representing 30%, 27%, and 23% of the MOA, respectively. Collectively, >80% of known occupied area occurs in these three states. Three other states (Montana, Utah and Oregon) each have occupied areas >1500 km^2, representing 6-7% of the MOA, while both California and Colorado contain <200 km^2 each (0.6% and 0.3% of the MOA, respectively). The distribution of known occupied areas across the range suggests greater occupation of the northern and eastern portions of the geographic range (Fig. 1b), however, these patterns could be influenced by variation in sampling effort.

Species distribution model

Our final model of habitat distribution for pygmy rabbits was built at the range buffer extent with a regularization multiplier of 1. In our analyses, AUC increased as the extent of background points increased (i.e., model AUC was highest at the range buffer extent and lowest at the 10 km buffer extent), and AIC values declined from the 10 km buffered to the range buffered modeling extents in general (Appendix D). Models with low (default) regularization multipliers at each extent had the greatest support from our data. AIC was lowest for models using a regularization multiplier of 1 and highest for models with a multiplier of 10 (Appendix D), and AUC decreased as regularization multiplier increased. In general, each of the 11 calculated threshold levels (values given as potentially useful cutoffs for distinguishing suitable and primary habitat) were significant ($\alpha = 0.05$) in binomial tests of omission across all models.

Variables included in our final model generally matched the current understanding of habitat requirements for this species. Although both AUC and AIC supported the most complex environmental variable structure (i.e., full models), the differences were relatively marginal (Appendix D, Appendix B). We chose a reduced model because models built with many (in our case 39) environmental variables are challenging to interpret and repeatability can be limited. The most important variable influencing distribution of pygmy rabbits was the distribution of big sagebrush (percent contribution = 52, permutation importance = 18). Other influential variables included slope (percent contribution = 13, permutation importance = 16.3), elevation (percent contribution = 11.1, permutation importance = 8.2), and NDVI (percent contribution = 9.3, permutation importance = 6.4). Pygmy rabbits were associated with lower values for slope and NDVI, and intermediate elevations relative to the availability of these variable values across the study area (i.e., the full modeling extent). Three climate variables were retained in the final SDM; mean temperature of the warmest quarter (BIO 10; 10.1% contribution, 35.8 permutation importance), precipitation seasonality (BIO 15; 3.4% contribution, 9 permutation importance), and temperature seasonality (BIO 4; 1% contribution, 6.4 permutation importance).

Predicted primary habitat for pygmy rabbits covered >132,000 km^2 across the range of the species, but much of this area consists of fragmented patches of varying sizes and isolation (Fig. 2). We identified four relatively large core areas (>21,000 km^2) of mostly contiguous primary habitat which we refer to as (1) eastern Idaho, (2) southwestern Wyoming, (3) northeastern Nevada, and (4) south-central Oregon. These names reflect the geographic center of each core area, but the primary habitat expands from these areas, forming irregular shapes and spanning state boundaries (e.g., the eastern Idaho core also includes southwestern Montana and is bisected by large mountain ranges). Wyoming, Nevada, and Idaho supported the greatest amount of primary habitat (40%, 24%, and 16%, respectively). As with the MOA, these three states contain >80% of predicted primary habitat for pygmy rabbits, with the remainder of this habitat category spread throughout the other range states. The Greater Green River Basin Section in southwestern Wyoming contains 24% of predicted primary habitat, the most of any ecological section in the study area.

Areas identified as suitable habitat (224,820 km^2) are generally located adjacent to primary habitat core areas, and in many cases, fill the gaps among fragmented patches of primary habitat (Fig. 2). In some areas, suitable habitat form corridors joining patches of primary habitat (e.g., in southeastern Idaho and central Utah). Suitable habitat corridors could be important in providing habitat connectivity, especially over high-elevation mountain passes or across watershed divisions and along foothills between mountain valleys.

Overlap with sage-grouse

As expected, most known occurrences of pygmy rabbits overlapped with the distribution of sage-grouse and were encompassed within HMAs, with some exceptions at the edges of pygmy rabbit geographic range. For known occurrences of pygmy rabbits, 93% (25,986 km^2) of the estimated MOA overlapped with sage-grouse based on distribution information compiled by Schroeder et al. (2004). Given the much larger (~670,000 km^2) area estimated to be occupied by sage-grouse, pygmy rabbits were documented in only ~4% of the sage-grouse distribution. Land management designations for sage-grouse conservation (HMAs of any type) encompassed 92% (25,876 km^2) of the estimated MOA for pygmy rabbits. The remaining 8% of the MOA not included in any HMA was generally close to the periphery of the species range in southern Utah (Utah High Plateaus and Mountains and Southeastern Great Basin sections), California (Sierra Nevada and Mono sections), Oregon (Eastern Cascades, Modoc Plateau, and High Lava Plains sections), and the Montana-Idaho border (Beaverhead Mountains Section; Fig. 3). These seemingly unprotected areas of occurrence were highest in the Idaho-Montana border area. The Beaverhead Mountains Section includes 622 km^2 of MOA that is not within an HMA, which represents 28% of all of the MOA that does not fall within an HMA boundary and about 2.5 times more than the next most unprotected Section, the Central Great Basin Mountains Section (241 km^2). Idaho alone contains 48% of all of the MOA outside of HMAs. Additional overlap statistics for specific types of HMAs are summarized in Tables 3 and 4.

Predicted habitat distribution for pygmy rabbits also overlapped substantially with areas used by sage-grouse. We estimated that 88% (196,777 km^2) of suitable habitat and 91% (131,994 km^2) of primary habitat for pygmy rabbits overlapped current sage-grouse range as estimated by Schroeder et al. (2004). Predicted pygmy rabbit habitat falling outside of the estimated distribution of sage-grouse occurs mostly in small patches on the periphery of the geographic range (e.g., Beaverhead Mountains, Wind River Mountains, Utah High Plateaus and Mountains, Mono, and Modoc Plateau sections), but also in more central regions such as the Northeastern Great Basin and Overthrust Mountains (Table 4). Sage-grouse have a much larger geographic range than pygmy rabbits (e.g., most of Montana and Northern Wyoming are within the sage-grouse geographic range but outside of pygmy rabbit geographic range), but even within the bounds of shared geographic ranges for these two sagebrush obligates, there are large areas of unsuitable habitat for pygmy rabbits, according to our model. The southeastern corner of Oregon (Northwestern Basin and Range and Owyhee Uplands sections), north-central Nevada (Northern Lahontan Basin Section), and much of the fragmented patches of sage-grouse distribution in Utah and Colorado were not classified as suitable for pygmy rabbits by our model (Fig. 2).

The current organization of HMAs includes much of the predicted habitat for pygmy rabbits, and consequently, has the potential to function as an efficient conservation umbrella for pygmy rabbits. We estimated that 87% (194,738 km^2) of suitable habitat and 91% (132,189 km^2) of primary habitat for pygmy rabbits is contained within sage-grouse HMAs. Of the area modeled as primary habitat, approximately 59% falls within PHMAs, 34% in GHMA, 4% in IHMA, and 3% in OHMAs. This distribution of primary habitat across HMA types also mirrors the proportional distribution for suitable habitat for pygmy rabbits within HMAs (Table 1). Sections where the HMA umbrella falls short of protecting primary habitat for pygmy rabbits include the Yellowstone Highlands (1,091 km^2 outside of HMAs), Northwestern Basin and Range (1,104 km^2), and by far the most, the Beaverhead Mountains (2,912 km^2). On average, ecological sections within our study area have ~387 km^2 of primary habitat that is not encompassed under HMAs. Montana, Wyoming, and Idaho have the majority of primary habitat outside of HMAs (29%, 26%, and 21%, respectively; Table 4; Fig. 2).

Priority HMAs provide the highest level of habitat conservation, and these lands overlapped with suitable habitat, primary habitat, and MOA more than GHMAs. PHMAs contained 59% of primary habitat, whereas only 34% fell within GHMAs. Although GHMA area across the 10 western states is 1.2 times greater than that of PHMAs, within our study area, PHMA area exceeded GHMA (also by 1.2 times). Nonetheless, the proportion of primary habitat in an HMA type relative to the HMA area within our study area boundary was

0.41 for PHMAs and 0.28 for GHMAs, meaning that PHMAs included a greater proportion of primary habitat (Table 1). Additionally, IHMAs, which encompass intermediate-quality sage-grouse habitats in Idaho had a proportion of 0.31. These patterns are reflected in MOA as well; 61% of MOA overlapped with PHMAs while only 24% overlapped with GHMAs. These findings support the hypothesis that PHMAs, despite being designated for sage-grouse, also encompass high-quality habitats for pygmy rabbits. Therefore, even though HMAs do not encompass all pygmy rabbit habitat or known occupied areas, they have the potential to be effective conservation designations for pygmy rabbits. Efficacy of these designations for either species, however, will depend on land management within the HMA boundaries.

Discussion

We provide the first range-wide estimate of minimum occupied area by pygmy rabbits and a species distribution model predicting suitable habitat, excluding the reintroduced population in the Columbia Basin. These outcomes provide necessary benchmarks against which changes in distribution can be systematically assessed, and they allow an evaluation of the effectiveness of ongoing sage-grouse-focused land management in conserving habitat for pygmy rabbits. Our analysis suggests that the sage-grouse HMA umbrella has the potential to conserve pygmy rabbits at the geographic range scale because areas occupied by and modeled as suitable habitat for pygmy rabbits overlapped substantially with lands designated as HMAs, although 8% of the estimated MOA and 9% of modeled primary habitat falls outside of HMAs. If land management goals retain intact sagebrush communities within the HMAs, then these areas are likely to also support conservation of pygmy rabbits.

Occurrence of pygmy rabbits

Despite petitions for ESA listing dating back to 2003, this work provides the first comprehensive dataset of the occurrence of pygmy rabbits. Recent occurrence locations were recorded in eight states in the western USA (Wyoming, Idaho, Nevada, Montana, Oregon, Utah, California, and Colorado). Based on our estimates of the MOA, Wyoming, Idaho, and Nevada support the majority of known populations and consequently, likely have the greatest potential for species conservation (Fig. 1b). However, surveys for pygmy rabbits in novel areas within all range states could change our understanding of their distribution in the future.

As expected, the current distribution of pygmy rabbits is highly patchy within their geographic range. The most isolated patches occur in south-central Utah, in California's Mono Basin, along the border of California and Oregon, and in two areas in Northern Oregon (Fig. 1b). In the central portion of the species geographic range, we noted large gaps in distribution, both in terms of occurrences and modeled habitat. Specifically, there are gaps in northern to central Utah and western Nevada that coincide with Pleistocene epoch lakes Bonneville Lahontan. The distributions of both sagebrush and occurrences of pygmy rabbits appear to be negatively correlated with the distribution of these prehistoric lakes, possibly due to climactic changes in the middle Holocene that altered vegetative communities (Grayson 2000; 2006, Schmitt et al. 2002) and potentially soil characteristics in these basins.

Our estimate of the recent area occupied by pygmy rabbits throughout their range (28,366 km^2) is based on 3-km buffers around occupied locations recorded since the year 2000 (n = 10,420). This method produced patches that were circular in shape around isolated occurrences, however, elongated patch shapes were common in basins or mountain valleys, especially in regions dominated by basin and range topography (e.g., east-central Idaho and Nevada). The 3 km buffer is linked to movement ecology of the species, however, the estimate of the MOA should be considered in the context of this decision, which might be re-evaluated in the future with movement data from individuals in other regions of the species range. Future estimates of the MOA also could increase if new records of occurrence are confirmed and decrease as a function of habitat loss (e.g., through fires or land conversion) or population extirpations.

Species distribution model

As expected, the final SDM was consistent with general results from studies of habitat selection by pygmy rabbits conducted at more local spatial scales. The most important variables included distribution of big sagebrush (Table 2). Sagebrush vegetation is central to pygmy rabbit survival as a food source and the primary structural component of their habitat, and both density and height of sagebrush have been consistently associated with habitat use by pygmy rabbits (Green and Flinders 1980, Weiss and Verts 1984, Katzner and Parker 1997, Heady and Laundré 2005, McMahon 2017). Sagebrush height was not a strong predictor in our SDM, which is likely a function of variation in shrub height across the pygmy rabbit range. Although pygmy rabbits select relatively tall shrubs within an area, the absolute height of sagebrush shrubs used by rabbits differs markedly across study areas (e.g., sagebrush used by rabbits in east-central Idaho was 2-29 cm [Parsons 2016] whereas heights >100 cm characterized habitat used in Northern Nevada [Larracea and Brussard 2009]).

Our model of predicted habitat suitability for pygmy rabbits identified variability across the geographic range that can be used as a tool for land management and conservation planning (Fig. 2). For example, Wyoming had the highest ranking in our analyses of both the MOA and area predicted as primary habitat for pygmy rabbits, but Nevada ranked second highest in primary habitat despite having less estimated MOA than Idaho. Patterns like these might reflect imprecise estimates of habitat suitability, the fact that pygmy rabbits are absent from some areas of suitable habitat, or spatial variation in survey efforts. Areas of predicted primary habitat that are outside of MOA could be identified as places to focus field surveys for pygmy rabbits. Documenting areas previously but not currently occupied by pygmy rabbits could shed light on trends in sagebrush degradation and help with early detection of population declines.

We identified four relatively isolated core areas of primary habitat throughout the geographic range of this species (i.e., the eastern Idaho, southwestern Wyoming, northeastern Nevada, and south-central Oregon core areas). Although suitable habitat was identified in smaller patches between the core areas, their disjunct distribution coupled with relatively limited dispersal ability of this species likely results in barriers to population connectivity among the core areas of primary habitat. Indeed, the general distribution pattern of the four core areas is spatially consistent with divisions among sage-grouse populations and patterns of genetic diversity represented by microsatellite clusters (Connelly et al. 2004; Oyler-Mccance et al. 2005), which suggests that habitat distribution might result in shared barriers for both sagebrush-dependent species. Landscape genetic analyses for pygmy rabbits could test this idea and evaluate whether or not conservation of sagebrush corridors between these areas could provide avenues for gene flow at the geographic range scale. The distribution of these four core areas should be considered in ecosystem conservation plans and large-scale habitat management decisions.

Resolution and accuracy of soil data likely prevented soil characteristics from contributing more to our model predictions. Soil characteristics such as depth, type, and strength that are conducive to burrowing and holding burrow structure for long time periods are known to influence pygmy rabbit occurrence (Weiss and Verts 1984, Katzner and Parker 1997, Heady and Laundré 2005, Parsons et al. 2016). Yet, contrary to our expectations, few of these variables were retained in our final model, and those that were contributed relatively little to model predictions. Burrow systems are usually found in loamy, friable soils, favorable for digging (Weis and Verts 1984), and the selection of heterogeneously distributed soils likely contributes to the patchy distribution of the species on both coarse and fine scales (Weiss and Verts 1984). Such soils not only facilitate burrowing, but also growth of dense, tall sagebrush stands (Winward 1980, Davies et al. 2011). Because soil data for the entire extent of our study area is relatively coarse, our model likely under-valued the role of soils in shaping distribution of pygmy rabbits and their habitats.

Like most spatial models, several assumptions likely influenced our results. First, species distribution models assume that a species is in equilibrium with the amount of suitable habitat available, however, this might not be valid for pygmy rabbits because of dispersal limitations or high predation rates (Wiens et al. 2009). Consequently, our model includes commission errors, or classification of unoccupied areas as suitable due to favorable habitat characteristics. Second, the broad extent of our study necessitates reliance on remotely sensed data that include inherent spatial error. Third, survey effort for pygmy rabbits was not evenly distributed throughout the study area, even though we subsampled occurrence records to reduce the potential for sample bias. Fourth, variation in habitat selection at finer spatial scales could obscure broader scale patterns (Hällfors et al. 2016; Ikeda et al. 2017). Our model was built using the finest resolution feasible for our study area (i.e., 30 m resolution) resulting in a predictive map of >1.3 billion cells. However, the ability of pygmy rabbits to select habitat at very fine-scales means even a model generated using the finest resolution feasible will contain some errors. Finally, the choice of thresholds in SDM is problematic and an area of debate (Merow et al. 2013, Liu et al. 2016), and the extent of suitable habitat we defined is influenced by our choices for cut-off values (Appendix C). In our opinion, marginally better AUC and AIC scores did not justify the large number of variables retained in the full models, and suggestions from SDM literature include limiting complexity based on study objectives, data attributes, and understanding of the biological processes within the study area (Merow et al. 2014).

In one case, we made a modeling decision based on our knowledge of pygmy rabbit biology that did not strictly follow our process of variable reduction. Two variables (mean temperature of the coldest quarter and mean temperature of the warmest quarter of the year), were both highly influential and highly correlated, and we chose to include the warm quarter mean temperature, despite the fact that models usually ranked cold quarter mean temperature higher in percent contribution and permutation importance values. This decision was influenced by several lines of evidence suggesting that although overall thermoregulatory costs are higher in winter than in summer, pygmy rabbits exhibit behaviors that likely facilitate survival in cold temperatures but are less effective in hot conditions. Pygmy rabbits can buffer thermoregulatory costs by shuttling between burrows and the ground surface during winter, but such movements were not energetically beneficial during summer because burrow temperatures remained below their thermal neutral zones (Milling et al. 2017; 2018). Additionally, modelling efforts by Leach et al. (2015) predicted that the climactic envelope of pygmy rabbits relied heavily on maximum temperature (permutation importance 25.2%) in comparison to minimum temperature (permutation importance 0.0%).

Overlap between sage-grouse and pygmy rabbits

Our synthesis of recent occurrences of pygmy rabbits and our model of predicted habitat for the species demonstrate substantial overlap with the distribution of sage-grouse and grouse-focused HMAs. Given the obligate nature of both species with sagebrush, this finding was expected and is consistent with results of other regional studies. For example, Rowland et al. (2006) evaluated the utility of the sage-grouse umbrella in the Great Basin for 39 species, and documented extensive overlap of land cover associations between pygmy rabbits and sage-grouse based on ϕ (phi) correlation coefficients (mean $\phi = 0.84$). Similarly, out of 52 vertebrate species in Wyoming, predicted habitat for pygmy rabbits had the second highest degree of overlap with sage-grouse core areas (now called HMAs; Carlisle et al. 2018). Our study extends these efforts and provides a comprehensive evaluation of the potential for the sage-grouse HMA umbrella to protect pygmy rabbits at the range-wide scale.

Our results support the current distribution of sage-grouse HMAs as a potential conservation umbrella for pygmy rabbits based on overlap in both species occurrence and predicted suitable habitats. Both pygmy rabbit MOA and their predicted habitat are contained to a high degree within these lands (92% of MOA, 87% of suitable habitat, and 91% of primary habitat); furthermore, PHMAs, which are usually centrally located areas of high-quality sagebrush habitat, encompassed the greatest proportion of predicted habitat for pygmy rabbits. These results suggest that the current prioritization of HMAs may be well suited to pygmy rabbit conservation as PHMAs are designed to eliminate or extensively limit habitat disturbance (BLM 2015). However, these designations are not permanent, as are some other management designations (e.g., national parks, wildlife refuges, etc.), and they are open to exceptions in use as well as boundary changes.

Additionally, our results suggest that certain places in Idaho (i.e., the Beaverhead Mountains Section and other Sections in the Southeast corner of the state), Nevada (i.e., Central Great Basin Mountains Section), and Utah (i.e., Utah High Plateaus and Mountains Section) may require extra measures to protect areas occupied by pygmy rabbits (Fig. 1b). Similarly, places in Wyoming (i.e., Overthrust Mountains and Wind River Mountains sections), Nevada (i.e., Northeastern Great Basin Section), and southwestern Montana have large areas of primary habitat outside of HMA designation (Table 4). These areas could be targeted for pygmy rabbit surveys, and if populations are documented, would be candidate locations for additional habitat conservation measures.

Conclusion

One criterion for not conferring ESA protection for pygmy rabbits across the species range was the contention that their geographic range has not changed (Federal Register 2010). However, the patchy nature of their distribution and a lack of range-wide occurrence data mean that the information necessary to test this hypothesis did not exist. As new information (e.g., newly confirmed locations of pygmy rabbits, changes to habitat, etc.) becomes available across the western USA, the occurrence database can be updated along with estimates of MOA and the species distribution model. Our model also can be used as a tool to delineate areas for future surveys of pygmy rabbits. For example, areas where suitable habitat is predicted but records of occurrence are lacking could be targeted for field surveys. Additionally, the species occurrence data and distribution model could help to identify potential corridors of connectivity among larger, occupied areas and targets for conservation or habitat restoration, as needed. With more detailed and region-specific occurrence information, managers might be able to determine where source and sink populations exist and design conservation plans accordingly.

Umbrella strategies are used as simplified conservation tools partly because species that require large areas facilitate the protection of co-occurring species, and umbrella species strategies may help prioritize habitat remnants for conservation (Wilcox 1984; Noss 1990; Fleishman et al. 2000). Carlisle et al. (2018) simulated randomly distributed sagebrush “reserves” of the same size as sage-grouse Core Areas (a previous designation of HMAs) in Wyoming and evaluated overlap with distribution models for other sagebrush-associated wildlife. They reported that only 12 out of 52 species attained greater protection under designated Core Areas than within randomly simulated reserves. These twelve were primarily avian species, but also included other taxa that are strongly tied to sagebrush like the pygmy rabbit and species with relatively large distributions (Carlisle et al. 2018). These authors concluded that total protected area was key to the efficacy of the sage-grouse umbrella, and that this single species strategy would be effective for some, but not all sensitive species (Carlisle et al. 2018).

Sage-grouse umbrella conservation may indeed be a sufficient tool for designating areas for habitat conservation for the pygmy rabbit at the range-wide scale, although pygmy rabbit occupied areas and suitable habitat patches outside of HMAs may need additional conservation attention. Finer-scale analyses from smaller study areas (e.g., regional SDMs) might change understanding about patterns of overlap between sage-grouse and pygmy rabbits. Pygmy rabbits are relatively limited in their dispersal abilities compared to sage-grouse, which move to different habitats seasonally; consequently, spatial overlap in species distribution between these two sagebrush obligates might vary by season. Additionally, certain environmental variables such as soil characteristics might influence the regional distribution of pygmy rabbits, but have relatively little influence on sage-grouse. Conservation and management of sagebrush steppe communities will benefit from investigations into these dynamics across a diversity of scales.

Finally, pygmy rabbits are predicted to experience range contractions, regional extirpations, and possibly extinction by 2080 according to current climate change modeling (Leach et al. 2015). Climate modeling predicts that longer drier summers of increased evapotranspiration may negatively impact sagebrush communities because these ecosystems have a tight relationship with precipitation seasonality and will be limited in soil water during particularly dry summers (Schlaepfer 2012, Palmquist 2016). Range contractions for pygmy rabbits under climate change are predicted to be driven, in part, by rising temperatures and one estimate of the possible spatial distribution of future habitat for this species given expected climate change (Leach et al. 2015) is relatively similar to the distribution of the four core areas in our SDM (Fig. 2). A better understanding of species trends under climate change is needed for the sagebrush biome if land managers are to succeed in conserving this ecosystem and the services it provides. Although broad scale, single-species conservation strategies, like the sage-grouse umbrella, are attractive due to their simplicity, additional conservation measures targeting multiple species and scales will likely benefit long-term maintenance of biodiversity and resilience of the sagebrush ecosystem.

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Table 1.1: Extent of sage-grouse Habitat Management Areas (HMA) within the study area (Fig. 1a) and overlap with pygmy rabbits by HMA type. Minimum occupied area (MOA) by pygmy rabbits was estimated with a 3km buffer around trusted occurrences, and suitable and primary habitats for pygmy rabbits were estimated using an inductive species distribution model.

HMA Type	Range states	HMA within Study Area (km^2)	MOA (km^2)	Suitable Habitat (km^2)	Primary Habitat (km^2)
Priority	All	189,329	17,336	109,968	77,437
General	All	162,811	6,922	68,137	45,090
Important	Idaho	18,281	1,280	8,663	5,626
Other	Nevada, California	35,790	559	7,827	3,935
Linkage Connectivity	Colorado	984	0	139	98
Anthro Mountain	Utah	170	0	3	0.1
All HMAs	All	407,365	26,097	194,738	132,189

Table 1.2: Environmental variables included in the final species distribution model for pygmy rabbits across 8 western states and the percent contribution of each variable. Appendix A details variables, definitions, relevant geoprocessing steps, and data sources.

Environmental Variables	% Contribution	Permutation Importance
Big Sagebrush Distribution	52.0	18.0
Slope	13.0	16.3
Digital Elevation Model	11.1	8.2
Mean Temp. of Warmest Quarter (BIO 10)	10.1	35.8
Average Annual NDVI	9.3	6.4
Precip. Seasonality; Coefficient of Variation (BIO 15)	3.4	9.0
Temp. Seasonality; standard deviation *100 (BIO 4)	1.0	6.4

Table 1.3: Estimated minimum area occupied (MOA) and amount of predicted suitable and primary habitat (in km^2 and % of total) for pygmy rabbits in each of 8 range states in our study area. Also reported is the amount of primary habitat within designated sage-grouse Habitat Management Areas (HMAs) and the extent of HMAs by state. Range states: California (CA), Colorado (CO), Montana (MT), Oregon (OR), Nevada (NV), Wyoming (WY), Idaho (ID), and Utah (UT).

Range State	**MOA**	**Suitable Habitat**	**Primary Habitat**	**Primary within HMAs**	**State in HMAs**	**MOA Outside HMAs**	**Primary Habitat Outside HMAs**
CA	167 (<1%)	3,388 (2%)	1,476 (1%)	1,407 (1%)	11,743 (3%)	167 (8%)	69 (<1%)
CO	81 (<1%)	7,354 (3%)	4,035 (3%)	3,822 (3%)	13,784 (3%)	0 (0%)	213 (2%)
ID	7,693 (27%)	36,179 (16%)	23,441 (16%)	20,613 (16%)	60,066 (15%)	1,054 (48%)	2,822 (21%)
MT	2,006 (7%)	13,806 (6%)	9,752 (7%)	5,792 (4%)	11,131 (3%)	160 (7%)	3,960 (29%)
NV	6,374 (23%)	54,988 (24%)	35,518 (24%)	33,925 (26%)	113,014 (28%)	341 (15%)	1,594 (12%)
OR	1,556 (6%)	24,243 (11 %)	8,419 (6%)	7,770 (6%)	59,928 (15%)	196 (9%)	650 (5%)
UT	1,693 (6%)	9,655 (4%)	5,251 (4%)	4,537 (3%)	28,004 (7%)	289.6 (13%)	715 (5%)
WY	8,517 (30%)	75,203 (33%)	57,830 (40%)	54,320 (41%)	109,697 (27%)	4.5 (<1%)	3,511 (26%)
All	28,367 (100%)	224,819 (100%)	145,724 (100%)	132,185 (100%)	407,367 (100%)	2,212 (100%)	13,533 (100%)

Table 1.4: Estimated minimum occupied area (MOA) and primary habitat distribution for pygmy rabbits (in km^2 and % of total) by Bailey's Ecological Sections (Bailey 2016). Also reported is amount of MOA and primary habitat distribution that occurs outside of HMAs within each Section.

Ecological Section	MOA	Primary Habitat	MOA not in HMA	Primary Habitat not in HMA
Bear Lake	1,126 (4%)	4,320 (3%)	65 (3%)	110 (1%)
Beaverhead Mtns.	4575 (16%)	13,813 (10%)	622 (28%)	2,912 (22%)
Bonneville Basin	0 (0%)	156 (<1%)	0 (0%)	76 (1%)
Central Basin & Hills	1,017 (4%)	15,365 (11%)	0 (0%)	842 (6%)
Central Great Basin Mtns.	2,161 (7%)	9,525 (7%)	241 (11%)	772 (6%)
Challis Volcanic	1,000 4%)	2,470 (2%)	174 (8%)	266 (2%)
Eastern Cascades	51 (<1%)	0.8 (0%)	28 (1%)	1 (0%)
Greater Green River Basin	7,285 (26%)	15,365 (11%)	3 (<1%)	64 (1%)
High Lava Plains	191 (1%)	7 (0%)	60 (3%)	2 (0%)
Lahontan Basin	161 (1%)	98 (<1%)	11 (1%)	9 (<1%)
Modoc Plateau	28 (<1%)	1,300 (1%)	28 (1%)	59 (<1%)
Mono	147 (1%)	20 (0%)	137 (6%)	21 (<1%)
Northeastern Great Basin	1,736 (6%)	11,551 (8%)	44 (2%)	719 (5%)
Northwestern Basin & Range	3,976 (14%)	21,933 (15%)	161,7 (7%)	1,104 (8%)
Overthrust Mtns.	347 (1%)	3,314 (3%)	14 (1%)	953 (7%)
Owyhee Uplands	2,576 (9%)	9,659 (7%)	171 (8%)	333 (3%)
Sierra Nevada	32 (<1%)	0 (0%)	31 (1%)	0 (0%)
Snake River Basalts	1,048 (4%)	5,417 (4%)	139 (6%)	476 (4%)
Southeastern Great Basin	121 (<1%)	4 (0%)	97 (4%)	4 (0%)
Uinta Mtns.	49 (<1%)	2,205 (2%)	0 (0%)	160 (1%)
Utah High Plateau & Mtns.	711 (3%)	1,513 (1%)	185 (8%)	369 (3%)
Wind River Mtns.	31 (<1%)	1,165 (1%)	2 (<1%)	632 (5%)

Figure 1.1: (a) Location of study area and sage-grouse Habitat Management Areas (HMAs) in the western USA. The primary categories of HMA include Priority (PHMAs) and General (GHMAs) are shown and additional HMA types (Important HMAs (IHMAs), Other HMAs (OHMAs), Linkage Connectivity HMAs (LHMAs) and Anthro Mountain are merged together. (b) Bailey's Ecological Region Sections (Bailey 2016) within our study are numbered for reference. Estimated minimum occupied area (MOA) by pygmy rabbits in the western USA based on a 3 km buffer around trusted locations recorded since 2000. This buffer distance reflects the mean dispersal distance documented for this species (Estes-Zumpf and Rachlow 2009).

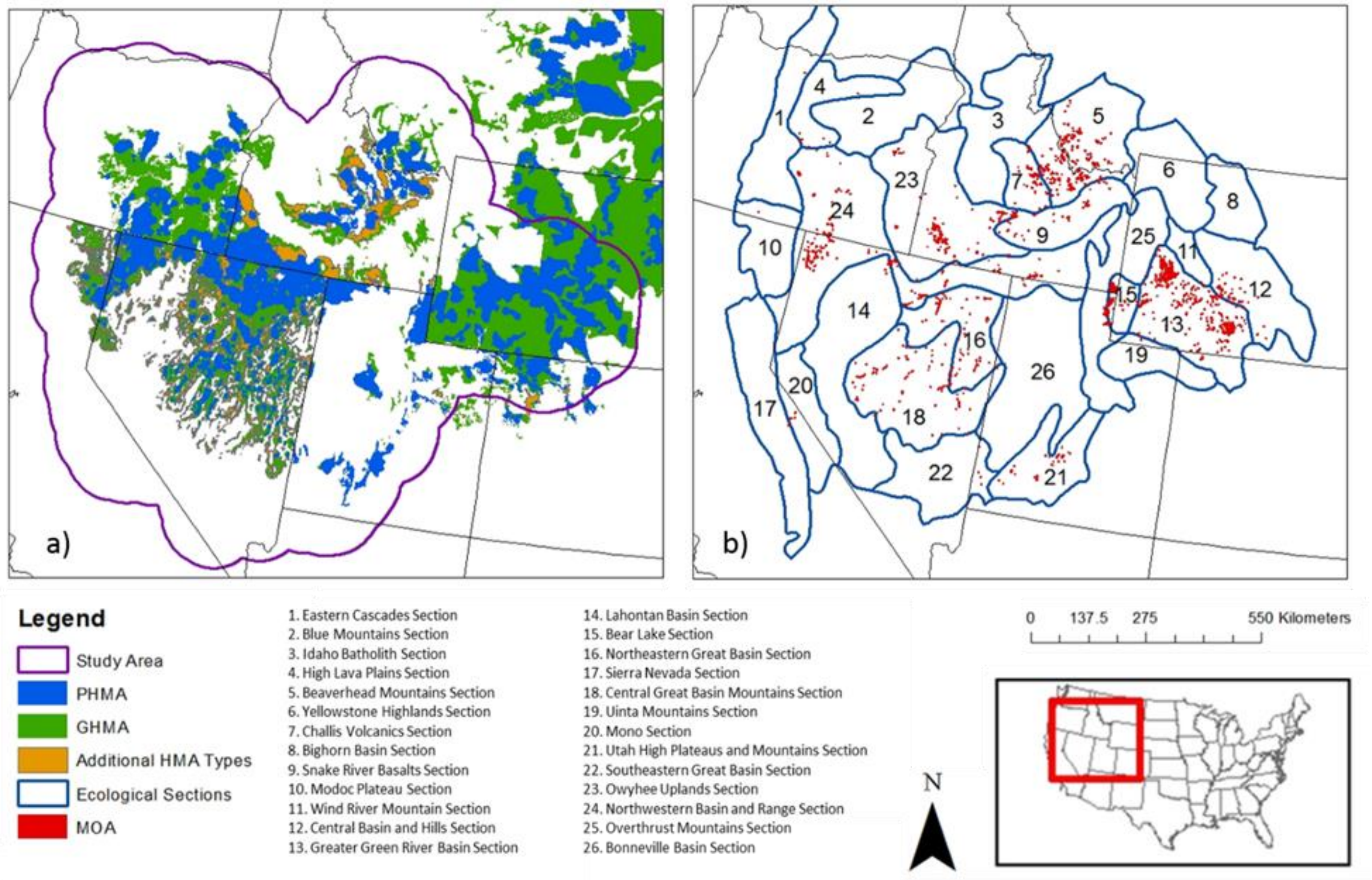


Figure 1.2: Predicted habitat for pygmy rabbits, categorized as suitable and primary habitat, using maximum training sensitivity plus specificity and equal training sensitivity and specificity thresholds, respectively. Four relatively isolated core areas of habitat were identified with largest area in Wyoming.

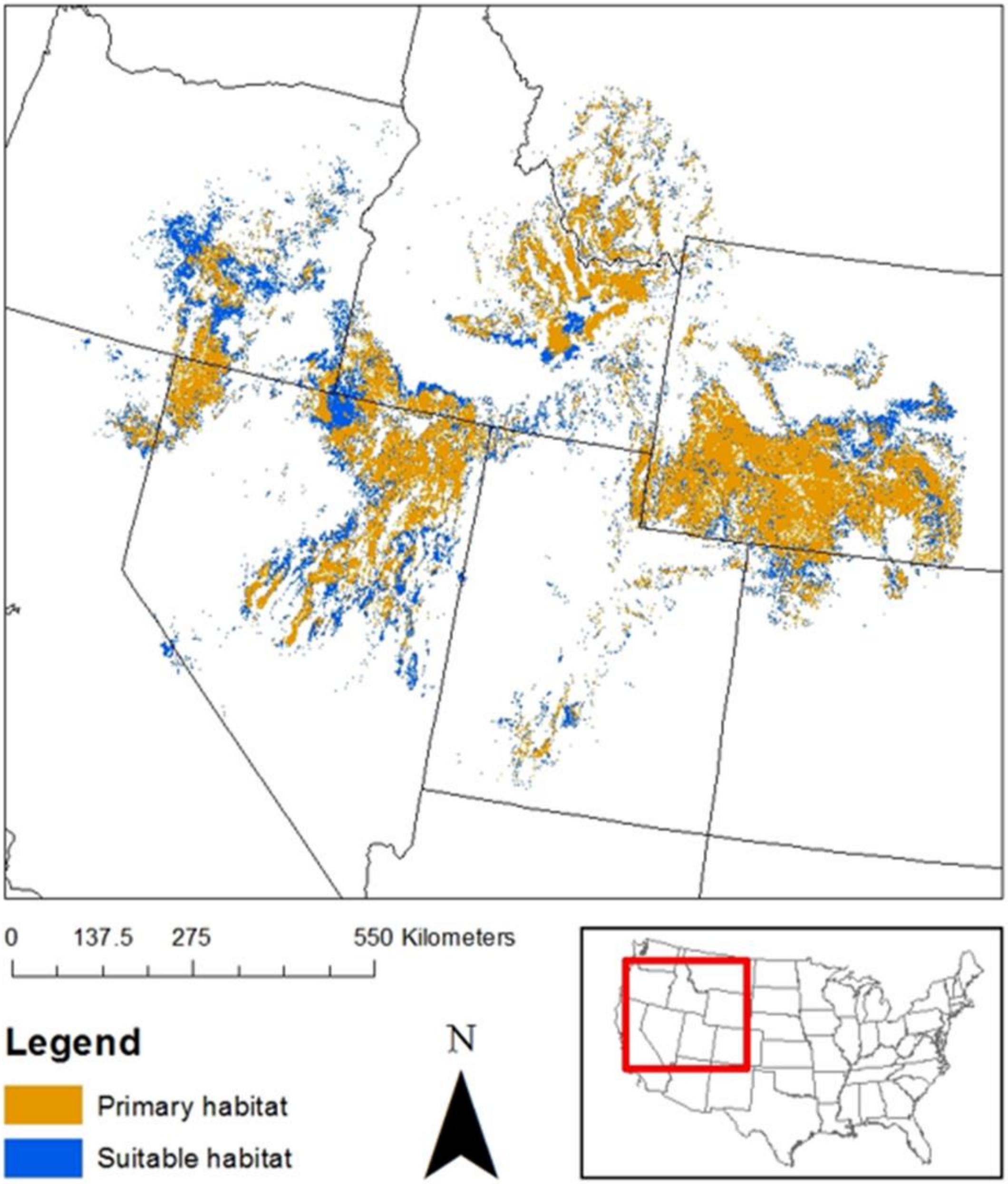
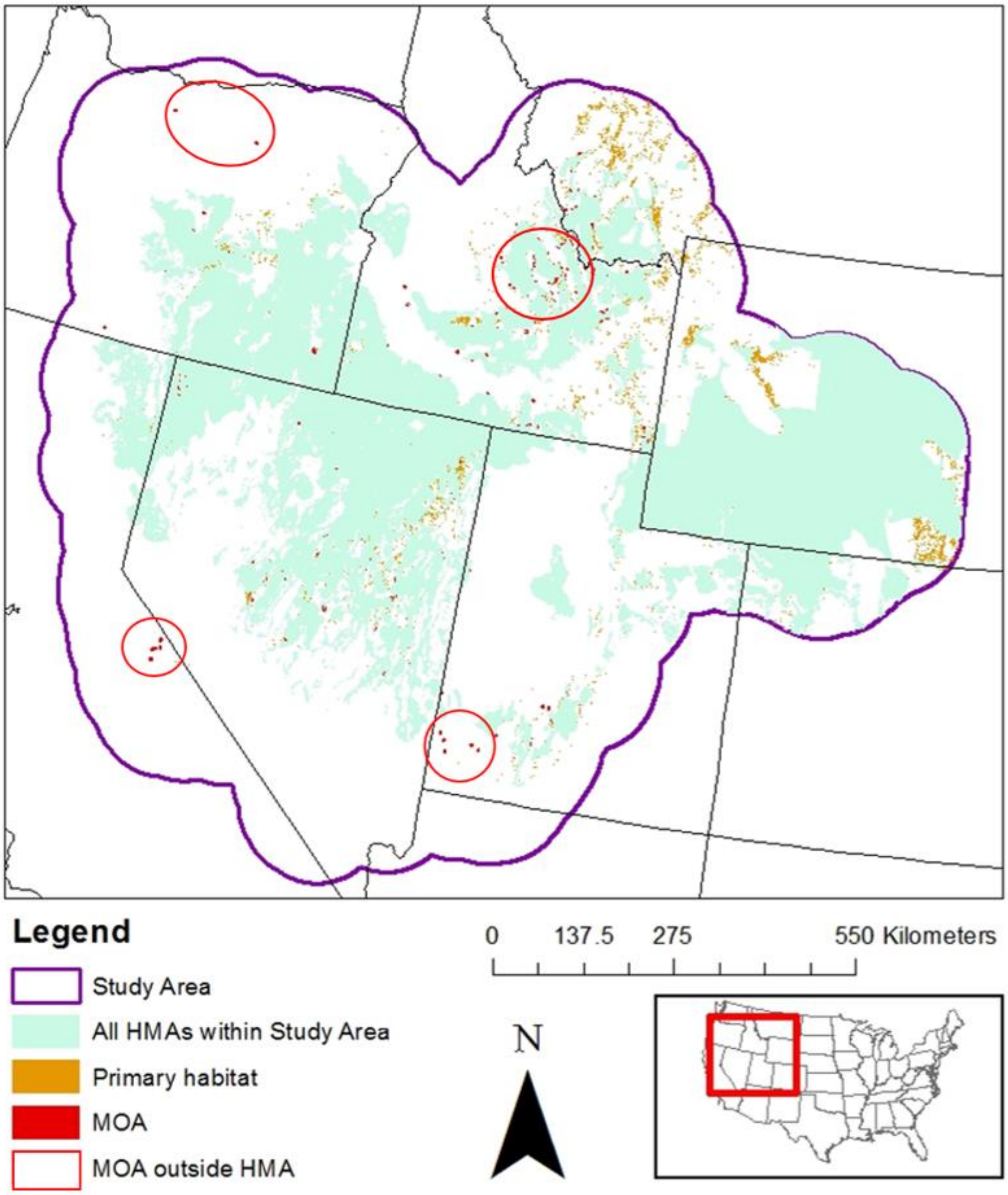


Figure 1.3: The overlay of both minimum occupied area (MOA) and primary habitat for pygmy rabbits with sage-grouse Habitat Management Areas (HMAs) can help identify potential areas for targeted conservation. Circled in red are a few of the currently occupied sites that are not protected by HMA designation.



Chapter two: Spatiotemporal Habitat Overlap in Sagebrush Basin and Range: An Assessment of Umbrella Species Efficacy

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Abstract

Although spatiotemporal scales affect ecological processes in diverse ways, their consequences are poorly understood in many circumstances. The utility of surrogate species concepts for management, such as umbrella species, depends on the co-occurrence of these species with target species of concern, yet the temporal and spatial scale at which this is assessed is rarely a subject of investigation. Greater sage-grouse (*Centrocercus urophasianus*) currently serve as an umbrella species for sagebrush ecosystems across the western USA, but this species migrates following different resource waves throughout an annual cycle. Our goal was to evaluate the degree to which sage-grouse seasonal habitat selection overlaps with habitat for another resident sagebrush species of conservation concern, the pygmy rabbit (*Brachylagus idahoensis*). We created an inductive species distribution model (SDM) for pygmy rabbits in east-central Idaho. We used maximum entropy methods to build models for both species incorporating a diversity of environmental factors representing topography, vegetation, fire, climate, and soil characteristics. We documented a relatively modest degree of spatial overlap between these species across the study area (50% of pygmy rabbit habitat within sage-grouse habitat) but less overlap when we evaluated specific seasonal models of sage-grouse distribution (18-31% of pygmy rabbit habitat in a given seasonal habitat for sage-grouse). Our models predicted that pygmy rabbits may occur in thin (1-2 km) sagebrush corridors between steep terrain features where sage-grouse usually are absent. Our sage-grouse models represent a rich location dataset and provide useful information to researchers and land managers alike. Additionally, the model of predicted habitat for pygmy rabbits can be used by land managers to prioritize locations for pygmy rabbit surveys and to identify areas for land management, conservation, or restoration efforts.

Introduction

Understanding factors that shape species distributions is critical to conservation planning, especially under changing environmental regimes. Like many ecological processes, drivers of species distribution differ across spatial and temporal scales (Ricklefs 1987, Wiens 1989). Climate and other abiotic variables often define broad geographic ranges (Austin 1980, Hawkins et al 2003, Thuiller 2003, Burrows et al. 2014), but other factors like disturbance, landscape features, and biotic interactions exert greater influence on species distributions at finer scales (Mackey and Lindenmayer 2001, Anderson et al. 2002, Phillips et al. 2006). Temporal dynamics of species distribution and co-occurrence also have been recognized as important biotic drivers of abundance and segregation, especially for migratory avian species (Abramsky and Safriel 1980, Deppe and Rotenberry 2005). Scale shapes ecological relationships and is important to consider in study design when investigating those relationships (Whittaker 2001, Rahbek 2005).

To be effective, approaches for conservation need to be developed and evaluated at appropriate scales, and often conservation activities are conducted at multiple scales (Schwartz 1999, Poiani et al. 2000). Although a focus on biodiversity assessment regularly necessitates broad scale approaches to identify broad patterns in species distributions (Meyers et al. 2000, Hughes et al. 2002, Brooks et al. 2006), habitat management and restoration activities are frequently designed and conducted at finer scales within regional geographic areas (states, provinces, or other jurisdictions). Information for conservation planning, implementation and assessment is needed at scales relevant to local regions and conditions (Gonthier et al. 2014, Groves et al. 2002, Moilanen et al. 2005).

Surrogate species strategies often are employed as streamlined approaches to address conservation objectives at broad extents because limited resources are available to study the resource needs of all species in an ecosystem. One such strategy, umbrella species, is commonly used to protect biodiversity and conserve habitats or ecosystems, thereby protecting sympatric species by encompassing their resource needs under a targeted set of rules and regulations without special consideration of each sympatric species (Caro and O'Doherty 1999, Roberge and Angelstam 2004; Caro 2003). This means that the umbrella species concept only works when the umbrella species has significant overlap in distribution with other species of concern, often leading researchers to model habitat similarity or map distributions to calculate overlap statistics (Caro 2003, Roberge and Angelstam 2004, Rowland et al. 2004). Although commonly ignored in overlap analyses, the temporal variation in species overlap is an important consideration.

Variation in temporal patterns of space and habitat use are common in seasonal environments, and behaviors such as migration have evolved in response to seasonal variation in resources (Hutchison and Maness 1979, Bradshaw and Holzapfel 2007). Although longer temporal scales (i.e., successional and climatic periods) have been addressed in species co-occurrence literature (e.g., Araújo et al. 2011, Tulloch et al 2016), relatively few studies have investigated the efficacy of migratory or seasonally mobile species functioning as umbrella or other surrogate species types (Favreau et al. 2006, Lindenmayer et al. 2002). Similarly, many analyses of species distribution and co-occurrence are conducted at relatively broad extents and coarse scales (Kunin 2000, Hartley 2004, McPherson 2006), but conclusions reached might not transfer to finer scales. Consequently, there is a need to evaluate spatiotemporal patterns of co-occurrence between umbrella species and the assumed sympatric species.

We explored the interaction between scale and umbrella species conservation by focusing on two habitat specialists of conservation concern in western North America; the greater sage-grouse (*Centrocercus urophasianus*) and the pygmy rabbit (*Brachylagus idahoensis*). The greater sage-grouse (hereafter "sage-grouse") is an iconic umbrella species that is driving one of the largest conservation efforts in USA history (Division of Corporate Affairs 2015). Sage-grouse occur only in sagebrush ecosystems in western North America, and historically, their estimated distribution encompassed 120 million km^2, but occupied range has declined by an estimated 56% to ~670,000 km^2 (Schroeder et al. 2004). Past studies have quantified spatial overlap and co-occurrence between sage-grouse and mule deer (Copeland et al. 2014), songbirds (Hanser and Knick 2011), reptiles (Jefferies et al. 2019), and multiple species assessments have been conducted by Rowland (2006) and Carlisle (2018). The mammalian counterpart to the sage-grouse is the pygmy rabbit, which also occurs only in sagebrush habitats. The species is currently designated as a species of greatest conservation need or a species of concern in all 9 range states (USGS 2018). Although both species have been petitioned for threatened status under the Endangered Species Act (Federal Register 2004, Federal Register 2010), conservation efforts to date have focused on conserving habitat for sage-grouse with the expectation that habitat for other species, including pygmy rabbits, would be protected under a sage-grouse umbrella.

Both sage-grouse and pygmy rabbits are considered sagebrush obligates, and many aspects of their fitness are tightly coupled to the sagebrush ecosystem. Sagebrush (*Artemisia spp.*) constitutes ≥90% of winter diets and ≥30% of summer diets for both animal species (Wallestad and Eng 1975, Remington and Braun 1985, Shipley et al. 2006). The structure of sagebrush shrubs also provides cover for these species throughout the year. Sage-grouse typically nest under sagebrush and nest success is higher when nests are associated with sagebrush than with other shrub species (Connelly et al. 1991, Coates and Delehanty 2010). Similarly, pygmy rabbits, which are obligate burrowers, often excavate burrow systems under sagebrush. Although sage-grouse and pygmy rabbits are both dependent on sagebrush throughout the year, their resource needs likely differ, at least during some periods of the annual cycle.

Unlike pygmy rabbits, sage-grouse shift patterns of habitat use across the year in response to availability of forage resources and reproductive activities (Connelly et al. 1991, Dalke et al. 1963, Connelly et al. 2000). During the spring sage-grouse gather at traditional lek sites for mating, and then females leave leks to initiate nesting in areas with both sagebrush cover (15% - 25%) and herbaceous understory (>15%) that provide both cover for their ground nests and forage (Connelly et al. 1991, DeLong et al. 1995, Connelly et al. 2000, Coates and Delehanty 2010). During the late brood-rearing season, sage-grouse follow phenological shifts in availability of herbaceous forage and insects, which are important food for chicks (Klebenow and Gray 1968, Drut et al. 1994). As vegetation desiccates during summer, sage-grouse move to either higher elevation sites or to mesic habitats with abundant forbs, including agricultural lands, wet meadows, and riparian areas. During the transition between summer and fall, sage-grouse shift to a diet of primarily sagebrush and generally form larger flocks segregated by sex (Braun et al. 2005). Winter habitat is characterized by a combination of favorable topographic, snow, and sagebrush vegetation traits. Sagebrush stands with ≥20cm above snow level and >10% cover are preferred, and areas of windswept snow such as ridgelines or hilltops, where sagebrush remains exposed are common roosting habitats during winter (Braun et al. 2005). Slope and aspect influences snow quality and depth, and southerly aspects are commonly selected by sage-grouse during winter (Back et al. 1987, Hubb and Braun 1989, Braun et al. 2005).

In contrast to sage-grouse, pygmy rabbits do not exhibit seasonal changes in habitat use. Two habitat features associated with the year-round presence of pygmy rabbits are relatively dense and tall sagebrush and soil characteristics that are conducive to burrowing, such as the presence of deep, loamy soils. At finer scales, pygmy rabbit populations often are associated with features such as alluvial fans, drainages, and micro-topography such as mima mounds that foster relatively deep soils (Grinnell et al. 1930, Borell and Ellis 1934, Weiss and Verts 1984, McMahon et al. 2017). Because pygmy rabbits are obligate burrowers, fine-scale heterogeneity in soil properties likely shapes their distribution to a greater degree than sage-grouse.

At the scale of their geographic ranges, 91% of modeled pygmy rabbit habitat is within sage-grouse range (Smith et al. *in review*). Our goal for this study was to estimate species distributions and co-occurrence of sage-grouse and pygmy rabbits at finer spatial and temporal scales. We hypothesized that: H1) seasonal distributions of sage-grouse would reflect seasonal differences in resource selection. We expected that spring distributions would be influenced by greater sagebrush cover and a lack of forest canopy cover and agriculture. We predicted that higher elevations and greater vegetative productivity would characterize the late brood-rearing period, and that areas of relatively tall sagebrush and higher topographic roughness that foster heterogeneous snow conditions at fine spatial scales would characterize winter distributions; H2) distribution of pygmy rabbits would reflect vegetation and soil characteristics known to be associated with their habitat selection at fine scales. We predicted that pygmy rabbit habitat would be characterized by greater sagebrush cover and height, and soils that have loamy textures and medium porosities; H3) the two species would exhibit a high degree of overlap because of their strong association with sagebrush-dominated habitats. However, we expected overlap to be less at the finer spatiotemporal scales than the extensive overlap documented at range-wide extents (Smith et al. *in review*); and H4) degree of co-occurrence would differ among seasons because sage-grouse change habitat use seasonally but pygmy rabbits do not. We expected the greatest overlap during spring relative to the other seasons because sage-grouse select habitat characteristics that are most similar to pygmy rabbit preferences during that season (i.e., abundant sagebrush and productive areas of herbaceous cover).

Our approach used species distribution models (SDMs) with remotely sensed environmental data and location data for both sage-grouse and pygmy rabbits in east-central Idaho, USA. We created three seasonal SDMs for sage-grouse (spring, late brood-rearing, and winter) and one general distribution model pooled across all seasons (hereafter the "all-seasons" model). We also conducted field work to supplement location data for pygmy rabbits and to gather site-specific habitat information to help guide the development of the pygmy rabbit SDM. This work provides an evaluation of seasonal co-occurrence of two highly specialized species and demonstrates how putatively similar habitat needs can vary across time. The SDMs and analyses of overlap between these two sagebrush obligates can inform decisions about conservation strategies for sagebrush communities at regional scales that are relevant to habitat management.

Methods

Study Area

We focused our analysis on a region of co-occurrence of pygmy rabbits and sage-grouse in east-central Idaho, USA, along the border with Montana that is defined by basin and range topography, including multiple mountain ranges. This region (21,756 km^2) is adapted from the Mountain Valleys Conservation Area for sage-grouse identified in the Idaho Governor's Alternative and the approved resource management plan amendment published by the Bureau of Land Management (BLM) in Idaho (Idaho Governor's Sage-grouse Task Force 2012, BLM 2015).

Our study area encompassed a diversity of environmental characteristics, across an elevational gradient from 1,140 m to 3,754 m. At moderate elevations, spruce-fir forests (e.g. *Picea engelmannii* and *Abies lasiocarpa*) dominate mountain slopes and give way to Ponderosa pine (*Pinus ponderosa*) woodlands and mountain big sagebrush (*Artemisia tridentata ssp. vaseyana*) communities on the foothills. Sagebrush-steppe vegetation dominates the valley floors and rolling hills of the region; Wyoming big sagebrush (*A.t. ssp. wyomingensis*), black sagebrush (*A. nova*), low sagebrush (*A. arbuscula*), and threetip sagebrush (*A. tripartita*) are common foundation species in these areas. The region is considered high-elevation desert, and precipitation varies widely from mountain tops to valley bottoms; seasonal means range from 17 to 72 cm during winter and 10 to 150 cm during summer. Temperatures also are highly variable on both an annual and daily basis. Summer temperatures range between 45° C and -8° C and winter temperatures between 8°C and -16°C (PRISM, Version 14.1-20140502-1000; PRISM 2012).

Much of the study region is owned and managed by federal agencies including the BLM at lower elevations and the U.S. Forest Service (USFS) at higher elevations. Private lands occur most frequently on valley floors, and some areas with relatively deep soils near perennial water sources have been converted to agriculture or irrigated pastures. The dominant human use in this region is livestock grazing on both private and federal lands, and other land uses are primarily recreational activities (i.e., hunting, fishing, camping, and motorized and non-motorized travel).

Species Distribution Modeling

We used trusted occurrence locations for each species and environmental variables to create inductive models of the seasonal distributions of habitat for sage-grouse and annual distribution for pygmy rabbits using maximum entropy methods (Maxent 3.4.0; Phillips et al. 2006, Phillips and Dudík 2008, Phillips et al. 2017). Maxent characterizes conditions at occurrence sites, compares that environmental space to those available across the modeled region, and develops a continuous model of the relative likelihood of species presence based on the degree of similarity to occupied sites.

We modeled distributions of sage-grouse and pygmy rabbits using a common set of continuous variables that reflect land cover, landscape composition, topography, and late-summer vegetation greenness at multiple scales, plus additional soil and bioclimatic variables for the pygmy rabbit SDM (Table 2.1). While all model inputs were 90 m resolution gridded datasets, we used focal statistics to summarize metrics for various-sized neighborhoods based on species movements and ecology. At fine scales (45 m, 125 m, and 200 m radii), variables reflect the characteristics of an occupied site or an immediate neighborhood surrounding a location that encompasses the spatial uncertainty of some observation data. The mid-scale (1,000 m) reflects average daily movements of GPS-marked sage-grouse (IDFG 2018 unpublished data). The broadest scale (5,000 m radius) is consistent with Knick et al.’s (2013) analyses of landscape patterns and lek persistence as well as guidelines to protect breeding habitat for nonmigratory populations within 5km of occupied leks (Connelly et al. 2000). Topographic position indices were arbitrarily scaled between the fine and broad scales (500 m and 2,000 m radii). Bioclimatic variables, on the other hand, were simply resampled from 800 m to 90 m resolution. Although many of these variables were designed with sage-grouse in mind, they were still used in the pygmy rabbit SDM. Environmental data were downloaded and manipulated in ArcGIS 10.3.1 (ESRI 2016) and program R (R core team 2014).

Land cover

We incorporated vegetation land cover information that is known to influence the distribution of both sage-grouse and pygmy rabbits. We included 4 metrics related to sagebrush: mean canopy cover, mean sagebrush height, and the proportion of the landscape with at least 10% canopy cover at mid- and broad scales (1,000 m and 5,000 m radii). The 10% canopy cover threshold is related to the minimum requirements for sage-grouse winter habitat although breeding requirements are suggested to be higher at 15-25% (Connelly et al. 2000). Pygmy rabbits have been found in areas of sagebrush cover as low as 21% (Lee et al 2010, Camp et al. 2013). We also calculated mean tree canopy cover and the proportion of the landscape with >3% canopy cover at mid- and broad-scales, with the expectation that areas with tree canopy cover would be avoided. For example, Baruch-Mordo et al. (2013) documented population-level impacts to sage-grouse when conifer cover exceeded 4%. Lastly, we quantified the amount of agriculture at fine-, mid-, and broad-scales (200 m, 1,000 m, and 5,000 m), expecting that sage-grouse would also generally avoid intensive agriculture, even though they may use agricultural lands adjacent to sagebrush habitats during the late brood-rearing period.

Topography

We calculated mean elevation and terrain roughness at the fine-scale, and topographic position indices at 500 m and 2,000 m scales. Terrain roughness was calculated as the standard deviation of elevation, and topographic position indices are a normalized difference between elevation at a central point and the surrounding average elevation (Weiss 2001). Topographic features can influence animal habitat by altering growing conditions for vegetation and affecting weather at micro-sites, for example by diverting wind and snow. Although not always identified as important indicators of habitat quality, topography impacts biological processes, and these measurements are sometimes included as environmental variables in predictive models like SDM or niche models, partly because they can serve as a proxy for some processes operating at finer scales than interpolated bioclimactic raster grids (Guisan and Zimmermann 2000, Lassueur et al. 2006).

Soils

We estimated mean values of six soil characteristics (bulk density, calcium carbonate percentage, clay percentage, sand percentage, silt percentage, and pore size distribution) by averaging all depth bins within 1m (Chaney et al. 2016). We also evaluated data on depth to the restrictive layer, which was a single value and therefore not averaged. Pygmy rabbits are obligate burrowers (Green and Flinders 1980), and are often associated with loamy, friable soils that are favorable for digging. The presence of deep and loamy soils also tends to support relatively dense and tall sagebrush stands, so the heterogeneous distribution of these soils potentially contributes to the patchy distribution of the species by influencing burrowing ability and vegetation structure (Winward 1980, Weiss and Verts 1984, Davies et al. 2011). Relatively deep and friable soils may indirectly affect sage-grouse distribution but only by influencing vegetation, so we did not include soil variables in sage-grouse models.

Climate

Climate can affect both vegetation and soil characteristics especially in highly seasonal landscapes such as our study area. We did not include climate variables in sage-grouse models, partly because sage-grouse can and will move to microclimates that are favorable. In contrast, pygmy rabbits are relatively sedentary and must cope with the conditions at burrow sites, usually by moving in and out of burrows or sagebrush cover in response to thermal properties (Milling et al. 2017; 2018). Using monthly temperature and precipitation normals (i.e., long-term datasets describing average conditions from 1981-2010; PRISM 2012), we calculated 19 bioclimatic variables patterned after Hijmans et al. (2005). These variables have been used extensively in species distribution modeling and wildlife habitat modeling (e.g., Elith et al. 2006, Anderson and Gonzalez 2011, Stanton et al. 2011) including pygmy rabbits (Smith et al. in review) to capture the climactic envelope within which species persist (Appendix A).

Sage-grouse observations

As part of a larger study, we complied over 380,000 sage-grouse observations in and around Idaho from 73 datasets stemming from VHF and GPS telemetry studies, targeted sage-grouse surveys, and incidental observations. We carefully evaluated all data to ensure observational, spatial, and temporal accuracy. We retained only those records of live birds collected since 2000, for which potential error in coordinates was less than 400m, and dates could be attributed to a season (i.e., habitat use period). In addition, we reduced GPS records to 1 randomly selected location per bird per day. We also removed observations that coincided with mapped fire perimeters (BLM 2018) collected prior to or within 5 years following the fire discovery date, presuming that most fires were high-severity or stand-replacing and rendered the habitat unsuitable. This 5-year time lag was to account for potential use following a fire due to site-fidelity, and our assumption was that suitable habitat was present if birds continued to use these areas ≥5 years post-fire. After screening, we retained >53,000 observations of 875 marked birds and nearly 2,000 observations of unmarked birds in the study area to model general and seasonal distributions. For seasonal models we selected observations from spring (March 1–June 30; males and females), late brood-rearing (July 1–Sep 22; females, broods, and chicks only), and winter (Dec 1–Feb 29; males and females) habitat use periods. To reduce spatial redundancy and ultimately model processing time, we pooled nearby observations into occupied sites located at the center of an intersecting 90m grid cell. Additionally, for the all-seasons model, we further reduced locally dense sites by randomly subsampling with a minimum distance of 180m using SDMToolbox (Brown et al. 2018, Brown et al. 2017). Lastly, for each sample, we randomly withheld 20% of the sites for map classification, using the other 80% for model development (Table 2.2).

Pygmy rabbit locations

The study region had a relatively well-documented set of occurrence locations for pygmy rabbits (n >1,300) compared to other regions for which detailed sage-grouse information was available. Pygmy rabbit locations were collected from field surveys for burrows, reference locations for collection of pygmy rabbit specimens or photographs, and incidental records collected by state and federal biologists. Additionally, several studies of pygmy rabbit ecology have been conducted in this region, which contributed locations from live captures and radio telemetry (e.g., Sanchez and Rachlow 2008, Rachlow et al. 2010, Estes-Zumpf et al. 2010, Camp et al. 2013, McMahon et al. 2017). We screened all pygmy rabbit location information and only retained records that were trusted by wildlife agencies or that referenced confirmed evidence of the species (i.e., pygmy rabbit pellets at burrow sites, photographs, visual confirmation, or field specimen collection). We filtered the trusted locations using a distance of 800 m, which retained only one point per pixel for the coarsest resolution environmental data used in the pygmy rabbit SDM.

Model development and classification

We supplied Maxent with presence data described above, as well as background points (n=47,900 for sage-grouse, n=10,000 for pygmy rabbit) consisting of randomly generated pseudoabsences across the study area that were >180m apart and >180m from presence locations. In an iterative approach, we optimized each model for a regularization multiplier (a smoothing factor) by testing values from 0.5–20 and feature types (linear, quadratic, product, threshold, and hinge) using the *enmSdm* package (Smith 2019) in R 3.5.2 (R Core Team 2018). Increasing regularization reduces the overfitting of models and can help overcome issues of sampling bias and spatial autocorrelation in the presence data (Elith et al. 2011, Warren and Seifert 2011, Radosavljevic and Anderson 2014). We selected the best performing combination based on AICc (Warren and Seifert 2011, Wright et al. 2015) and constructed a full model inclusive of all variables (n = 13–16 for sage-grouse and n = 42 for pygmy rabbits) (Table 2.1). We implemented a 10-fold subsampling routine, using 70% of sage-grouse locations and 80% of pygmy rabbit locations for model training, the remainder for testing model fit, and jackknifing to measure importance of each variable to the resulting model. Using the average model across 10 runs, we ranked variables based on their permutation importance and removed those that were < 2%. We also removed highly correlated variables (Pearson's correlation >|0.8|), keeping the variable with the higher permutation importance. We repeated this process of model optimization, construction, and variable ranking until there were no highly correlated variables and all variables gained at least 2% permutation importance, usually in 2–4 iterations.

These final, reduced models were categorized into 4 habitat suitability classes: non-habitat, low suitability, moderate suitability, and high suitability habitat. We used two primary sources of information to choose thresholds for these habitat categories (Table 2.2). Standard output from a maxent model calculates 11 threshold values and binomial probabilities based on omission and predicted area. We also used the *ecospat* v3.0 R package (Broennimann et al. 2018) to calculate the continuous Boyce index for the validation dataset reserved for map classification. The Boyce Index compares the predicted values at validation locations to expected values based on the distribution of predicted model values, reporting an overall model fit (Spearman rank correlation that varies from -1 to 1) and a plot of Predicted/Expected ratio (*F*-ratio) versus habitat suitability (Hirzel et al. 2006). This plot can be used to determine the range of values where habitat is used less than available (avoided; non-habitat), suitable but used in proportion to availability (i.e., low suitability), more frequently than available (i.e. moderate suitability), and many times more frequently than available (i.e., high suitability). The threshold between moderate and high suitability classes can be subjective.

Species Distribution Overlap Calculations

We used multiple metrics to analyze spatial overlap between sage-grouse SDMs and the pygmy rabbit SDM and the factors affecting their co-occurrence. We calculated three metrics related to model overlap that are sometimes used to identify niche overlap: Pearson's correlation, Schoener's D (Schoener 1968), and the I statistic (Warren et al. 2008). These metrics all quantify similarity between species distributions and output a statistic on a normalized scale; Pearson's correlations range from -1 to 1, and both Schoener's D and Warren's I range from 0 to 1, with values closer to one representing higher overlap. Warren's I was developed specifically for presence only SDMs and calculates pairwise overlap between models. In contrast to older and commonly used Schoener's D, Warren's I treats individual species predictions as probability distributions with no biological assumptions (Warren 2008). We focused on overlap of high suitability habitat (also referred to as highly suitable habitat) and used these values to make inferences about the relative amount of shared habitat between the species by season.

To help interpret how environmental variables influenced each species, we developed response curves using our modeling points and environmental data. These curves illustrate occurrence probability for each species and seasonal occurrence for sage-grouse across the environmental gradients that were commonly retained in the final models.

Field Surveys

We used two preliminary models to stratify pygmy rabbit sampling sites for field surveys across habitat suitability categories; an all-seasons sage-grouse model developed in 2017 (IDFG unpublished data) and a pygmy rabbit model built with a different set of environmental information (Appendix A). We classified the preliminary models for each species into three categories (non-habitat, low suitability habitat, and suitable habitat), and we randomly distributed 1,111 points across the classification matrix: (1) suitable habitat for both species, (2) suitable habitat for only sage-grouse (i.e., non-habitat for pygmy rabbits), (3) suitable habitat for only pygmy rabbits (i.e., non-habitat for sage-grouse), and (4) areas of low suitability for both species areas. Samples were distributed proportional to the area in each category in our study region, and we attempted to visit sites across categories within each quadrant of our study region to obtain a spatially balanced representation of habitat types across the region. We did not conduct field surveys in areas considered to be non-habitat for both species.

We completed field surveys during May–August 2018 to collect new locations of pygmy rabbits and to record information about site-level vegetation and soil characteristics that influence distribution. Surveys included (1) a complete census of pygmy rabbit burrows within 1-ha plots to determine occupancy, (2) soil pits (depth ~70cm) to assess soil characteristics at the site level, and (3) a vegetation transect line consisting of 50 points. If no pygmy rabbit burrows and associated evidence (sighting of the animal or presence of pellets) was observed, we recorded the plot as unoccupied. If pygmy rabbit burrows were found, we counted the number of burrow entrances and recorded activity level based on a categorization scheme outlined by Roberts (2001). This rated burrows as either (1) active, (2), recently active, (3) old, or (4) very old based on quality of burrow entrance and freshness of pellets. The density of active burrows can be used as an index of relative abundance of the species (Price and Rachlow 2011). Vegetation and soil measurements and methods follow the Assessment, Inventory, and Monitoring (AIM) Protocol used by the BLM (Toevs et al. 2011). We also characterized plots based on the presence of sage-grouse sign (yes/no), mima mounds (yes/no), and trees (yes/no), as well as the general landform type (i.e., hillside, alluvial fan, valley floor, terrace, plateau, rolling plain, flood plain, playa, or ravine).

Field data, including soil, vegetation, and observed site characteristics were summarized by occupancy status of visited sites. This allowed us to draw inferences about how site level characteristics and individual environmental variables shaped habitat suitability. We also wanted to draw conclusions about how site level characteristics related to abundance of pygmy rabbits. We provide brief analyses of our preliminary pygmy rabbit model using data collected from the field.

Results

All-seasons model

The all-seasons model for sage-grouse (Figure 2.1a) was characterized by several vegetation and terrain features and included 6 environmental variables (Table 2.3) that closely aligned with our expectations. Three land cover variables were influential. The proportion of the landscape with >3% forest canopy cover (mid-scale) had the greatest influence, reflecting avoidance of trees by sage-grouse. Likewise, the proportion of land in agriculture (broad scale) also had relatively high percent contribution and permutation importance, indicating that grouse also avoided areas of dense agriculture. The proportion of the landscape with ≥10% sagebrush cover (mid-scale) was the only sagebrush variable retained in the model and positively associated with sage-grouse occurrence; mean sagebrush cover and the proportion of sagebrush (broad scale) were all dropped during the variable reduction process because they were highly correlated. Sagebrush height was not used in this model because of the seasonal changes expected throughout the annual cycle. Terrain roughness (occurrence declined sharply as roughness values increased from 0) and the topographic position index within 2,000 m both suggest that sage-grouse tend to select flat areas or middle slopes. Low to medium elevations (~1,500 m to 2,000 m) sites had the highest occurrence probability. The all-seasons model for sage-grouse had an AUC of 0.797, indicating a relatively high predictive performance, but higher omission and commission rates than the season-specific models (see below).

We used 4,081 validation sites to calculate model thresholds (Table 2.2) and classify relative habitat suitability (Figure 2.1a). Using the validation dataset, 24% of reserved sites were located in moderate habitat suitability, and 62% of occurrences fell within areas identified as highly suitable. Suitable areas in upper valley bottoms tended to be more fragmented than at lower elevations and also tended to occur on relatively low-angle slopes along the edges of the valleys. One of the largest patches of highly suitable habitat for sage-grouse was in the Upper Snake River Plain in the southeastern portion of our study region (Figure 2.1a); this area is a scrubland with few trees and relatively little agriculture. In contrast, there was relatively less highly suitable habitat identified in the western portion of the study region in general, and those patches were highly fragmented.

Spring model

The spring SDM for sage-grouse (Figure 2.2) was similar to the all-seasons model but also included sagebrush height and the topographic position index at the mid-scale (500-m radius). Observed occurrence probability during spring peaked at sagebrush heights ~27cm and where the more localized topographic position index was near 0 (Figure 2.3). Sage-grouse occurred in the largest range of sagebrush cover during this season. The spring model for sage-grouse had an AUC of 0.823 indicating relatively high likelihood of predicting presence locations to be higher suitability than absence locations. Our classification of the spring model resulted in habitat distribution maps that looked very similar to the all-seasons classification. Sage-grouse are widely distributed in the spring, especially in the Upper Snake River Plain but also in the mountain valleys. Highly suitable spring habitat (3,191 km^2) occurred in the high mountain valleys, but the largest patches were still in the southeastern portion of our study region (i.e., the Upper Snake River Plain, Table 2.4, Figure 2.2). Spring habitat patches were often bisected and fragmented by areas surrounding highways, rivers and streams, and other landscape features, a pattern that was not as apparent in other seasonal models.

Late brood-rearing model

All environmental covariates in the all-seasons SDM also were retained in the LBR model along with three additional ones: sagebrush height, average NDVI, and the standard deviation of NDVI. Sage-grouse habitat moved to more confined, higher elevation areas during the LBR period than other seasons (Figure 2.3), and average measures of NDVI with lower intra-seasonal variability were helpful in predicting sage-grouse occurrence during this season, consistent with our predictions. Observed occurrence for sage-grouse in relation to sagebrush height peaked at 45 cm. The LBR model had an AUC of 0.854 indicating high accuracy. Highly suitable LBR habitat (2,505 km^2) tended to be concentrated in large, isolated patches that were usually smoother in shape (i.e., less edge) than habitat patches in other seasons (Table 2.4, Figure 2.2).

Winter model

As was true for the other seasonal models, all variables in the all-seasons model also were retained in winter model (Table 2.3). Mean sagebrush and the proportion of agriculture in the immediate neighborhood also informed the winter model. Sage-grouse used a wide range of sagebrush heights during winter, but tended to be more frequently on the lower end than either spring or the LBR season. Unlike other seasons and the all-seasons model, the proportion of the landscape with ≥10% sagebrush cover (broad scale) was more important than at the mid-scale (Table 2.3). Sage-grouse occurred more often in landscapes with only 10% of land with sagebrush cover compared to lands with 50% of land with sagebrush cover at the mid-scale (Figure 2.3). As with other models, agriculture had a negative relationship with sage-grouse occurrence; the largest patches of highly suitable habitat in the winter were located in lower mountain valleys. As we predicted, topographic measures were helpful in predicting sage-grouse occurrence during winter; terrain roughness and topographic position indices were retained in the model much like the spring (Table 2.3). The winter sage-grouse model had an AUC of 0.911, indicating the strongest accuracy of all models created during this study. Highly suitable winter habitat for sage-grouse was the most spatially confined and limited in extent (1,521 km^2) compared to other seasonal models (Table 2.4, Figure 2.2). Highly suitable habitat was not extensively predicted in the Upper Snake River Plain.

Winter habitat was most similar to spring habitat except that it was lacking on the Upper Snake River Plain ($r = 0.783$, Table 2.5, Figure 2.2). Winter and LBR highly suitable habitats only overlapped by 72 km^2 (5% of winter highly suitable habitat) while winter and spring highly suitable habitats overlap by 1,026 km^2 (67% of winter highly suitable habitat, Table 2.4). Despite more divergence between spring and LBR habitats, these two seasons still shared 1,329 km^2 of highly suitable habitat (i.e., 42% of spring and 53% of LBR habitat overlapped (Table 2.4, Figure 2.2). Out of all seasonal models, the spring model was the most similar to the all-seasons model (r = 0.96, D = 0.898, I = 0.989, Table 2.5).

Pygmy rabbit SDM

Habitat for pygmy rabbits was characterized by 10 terrain, vegetation, soil, and climate variables (Table 2.3). Terrain roughness was by far the most important variable in the pygmy rabbit model, and pygmy rabbits are found at relatively low roughness values (Figure 2.3). As we expected, sagebrush characteristics strongly influenced the occurrence probability. Mean sagebrush cover in the immediate neighborhood and the proportion of landscape with ≥10% sagebrush within 5,000 m were retained in the model after variable reduction. Pygmy rabbit observed occurrence peaked at 19% sagebrush cover in the immediate area, and for the covariate representing the proportion of the landscape ≥10% sagebrush cover at the mid-scale, peaked at 55% (Figure 2.3). Like sage-grouse, habitat for pygmy rabbits reflected an avoidance of areas with trees. Two soil variables that reflect soil texture and permeability, silt percentage and pore size distribution (both with highest predictions at intermediate values, ~35% and ~0.37, respectively), were retained in the final model. Likewise, two bioclimate variables representing thermal extremes (the mean temperature of the warmest quarter and the mean temperature of the coldest quarter of the year) also were included in the model. Pygmy rabbits selected for intermediate values on both of these temperature gradients (~14° C for warmest quarter and ~-7.5° C for coldest quarter temperatures) suggesting avoidance of climatic extremes. The model AUC was 0.854 indicating high discriminatory power.

We classified the continuous pygmy rabbit SDM using three thresholds (Table 2.2) to delineate areas of relatively higher and lower predicted habitat quality (Figure 2.1b). Highly suitable habitat for pygmy rabbits tended to be located along the lateral edges of mountain valleys where slopes were generally less than 20 degrees and also at the upper ends of valleys, closer to headwaters and passes. Highly suitable habitat for pygmy rabbits also occurred in isolated sagebrush corridors that created thin strips between steeper mountainous terrain. Moderate suitability habitat usually buffered high suitability habitat at lower elevations, and low suitability and non-habitat filled the bottoms of mountain valleys, likely reflecting the prevalence of pastures in those regions where sagebrush has been reduced or removed.

Co-occurrence via Distribution overlap

As expected, there was considerable overlap between habitat for sage-grouse and pygmy rabbits in our study region. The predicted probability of occurrence for the sage-grouse all-seasons model and our pygmy rabbit model were positively correlated, but not to a degree usually considered high ($r = 0.66$, $p < 0.0001$, Table 2.5). Values for Schoener’s D and Warren’s I also were high (0.70 and 0.91, respectively). Almost half (49%) of the habitat identified as highly suitable for pygmy rabbits overlapped with highly suitable habitat for sage-grouse, but only about 29% of sage-grouse highly suitable habitat overlapped with that category for pygmy rabbits (Figure 2.4). Sage-grouse and pygmy rabbits shared the greatest amount of low suitability habitat (2,993 km^2), and a large amount of pygmy rabbit low suitability habitat was considered moderate (1,721 km^2) or high suitability habitat (1,100 km^2) for sage-grouse. Most overlap of highly suitable habitat for sage-grouse and pygmy rabbits occurred near the passes between the major valleys in the study region. Contiguous areas of highly suitable habitat for both species often were elongated areas stretching along the margins of valleys.

Contrary to our expectation that overlap between sage-grouse and pygmy rabbits would be highest during spring, LBR habitat had the greatest area of overlap of any seasonal sage-grouse SDM (712 km^2, Table 2.4). Correlation between LBR and pygmy rabbit habitat also was highest of seasonal habitats ($r = 0.60$, $p < 000.1$), as were Schoener's D and Warren's I (0.66 and 0.89, respectively). This season also had the most similar overlap ratios when we considered highly suitable habitat for each species as the denominator; 28% of sage-grouse and 31% of pygmy rabbit highly suitable was shared during the late brood rearing season (Table 2.4, Figure 2.4). Highly suitable habitat for sage-grouse was mostly absent from the thin, isolated sagebrush corridors between large mountains and hills that was predicted to be highly suitable for pygmy rabbits. However, these areas were more suitable during LBR than other seasons for sage-grouse. Overlap of LBR and pygmy rabbit highly suitable habitats occurred mainly in mountain valleys on the eastern portion of our study region and to lesser degrees in the valleys to the west.

Overlap of highly suitable habitat during spring (703 km^2) was less than LBR, despite having the greatest total area of predicted highly suitable habitat for sage-grouse during that season. Spring overlap had the second highest correlation value ($r = 0.58$, $p < 000.1$) and the second highest values for Schoener's D and Warren's I (0.66 and 0.88, respectively; Table 2.5). Given that more area was predicted as highly suitable for sage-grouse during spring, 22% of highly suitable habitat for sage-grouse and 31% for pygmy rabbits was encompassed within this spring overlap (Figure 2.4).

Winter habitat for sage-grouse overlapped the least (422 km^2) and had a relatively low correlation with pygmy rabbit habitat ($r = 0.45$, $p < 0.0001$); both Schoener's D and Warren's I were lowest for this season (0.53 and 0.8, respectively; Table 2.5). As opposed to other seasonal overlaps, a higher percentage of sage-grouse highly suitable habitat overlapped with pygmy rabbit habitat than the percentage of pygmy rabbit habitat that overlapped with sage-grouse habitat during winter (i.e., 28% of sage-grouse high suitable habitat overlapped with pygmy rabbit habitat and only 18% of pygmy rabbit highly suitable habitat fell within the overlapping area in winter). Overlap during winter was the most spatially dispersed of all seasons, and it occurred in relatively small patches.

Field Surveys

We surveyed 220 plots within our study region from 20 May to 5 August, 2018, and documented pygmy rabbit occupancy at 27 sites (~12%; Figure 2.5). One newly identified location was >5 km from the closest known population near Spencer, Idaho. New locations had an average occurrence probability of 0.60, although values ranged from 0.11 to 0.96. A *t*-test comparing predicted values from our preliminary model at occupied and unoccupied sites revealed a significant difference between these two groups (occupied mean = 0.58 and unoccupied mean = 0.43; $t = -2.17$, $p = 0.04$). Due to our low number of occupied sites, we did not evaluate abundance as a function of habitat characteristics.

Site-specific habitat characteristics at occupied and unoccupied locations were generally consistent with current understanding of pygmy rabbit ecology. However, we found no significantly different patterns between occupied and unoccupied sites ($p > 0.05$), with respect to geographic category, ground cover proportions, or vegetation growth type (Appendix E.). There was no significant difference between sagebrush height at occupied and unoccupied sites (averages of 49.7 cm and 51.7 cm, respectively, $t = -0.9556$, $p = 0.340$). At sites where sagebrush species were present, the mean percent cover of sagebrush ranged between 10% and 20%, and all sagebrush species found at unoccupied sites also were recorded in occupied sites with similar mean percent cover values (Appendix E.).

We found sage-grouse sign at 48 sites that we sampled (7 occupied and 41 unoccupied sites, Appendix F.). Of these sites, 5% were in low suitability habitat, 20% were in moderate suitability habitat, and 75% were in high suitability habitat, according to our all-seasons sage-grouse model. Trees were uncommon in all of our sample plots, in part because we only sampled locations considered as suitable habitat for sage-grouse or pygmy rabbits, and these species both avoid tree cover (Appendix F.). A higher proportion of sites occupied by pygmy rabbits had mima mounds (0.41) compared to unoccupied sites (0.25), but this was not statistically significant ($p>0.5$, Appendix F.).

Soil variables assessed in the field were similar between occupied and unoccupied sites. We averaged the rock percentage at each soil horizon to estimate an overall rock percentage, which was nearly identical across occupied (mean = 45.4) and unoccupied sites (mean = 45.5). When we grouped observed soil textures into three main categories (i.e., sand, silt, and loam), the distributions of soil textures was similar between occupied and unoccupied sites, with loamy soils being the most common at both types of sites (Appendix F.). However, when we retained all soil textures that we recorded as unique categories (i.e., clay, clay loam, sand, sandy clay, sandy clay loam, loamy sand, sandy loam, loam, silty clay, silty clay loam, and silty loam), sites occupied by pygmy rabbits were characterized by a high percentage of sandy clay loams, especially in the first horizon, relative to unoccupied sites (Appendix G.).

Discussion

We estimated species distributions for two sympatric, habitat specialists at relatively fine spatial and temporal scales to estimate how co-occurrence shifts across seasons. The sage-grouse has been the focus of conservation efforts for the sagebrush ecosystem in the western USA, and although overlap between sage-grouse and pygmy rabbits is high at the extent of the species range, we documented lower and variable co-occurrence at regional and seasonal scales. About half of high suitability habitat for pygmy rabbits in our study region was encompassed by the same habitat category in an all-seasons habitat model for sage-grouse, but estimated overlap decreased to 31% during LBR, 31% during spring, and only 18% during winter. To be effective, applications of surrogate species strategies (e.g., umbrella species) need to be developed and assessed at scales that are consistent with conservation actions. Our work suggests that even though pygmy rabbits, like sage-grouse, are tightly coupled with the sagebrush ecosystem, their conservation and management at regional scales might require additional consideration of habitats and locations outside of areas known to be primary sage-grouse habitat.

Our modeling of sage-grouse habitat was informed by a rich dataset (>55,000 locations) that facilitated quantifying seasonal variation in distribution. All four sage-grouse models included the same top three variables representing avoidance of trees, agricultural land cover, and steep or rough terrain (Table 2.3). Our study area can be visualized as semi-dichotomous; basins or large, rolling plains covered primarily by sagebrush steppe or agriculture (or other anthropogenic land use) and mountains covered by forests and rough terrain. Sage-grouse, predictably, prefer the basins and plains, and within these features, areas farther from agriculture. Other variables that influenced the distribution of sage-grouse in our models also support the notion that the sage-grouse is a landscape species as more mid to broad scale variables (n = 5) were retained in our sage-grouse models than variables characterizing land cover in the immediate neighborhood (n = 2). For example, proportion of land with ≥10% sagebrush cover at the mid-scale was retained while mean sagebrush cover at a fine scale (200 m radius) was dropped from the models. These habitat associations are consistent with a general understanding of sage-grouse habitat selection at broader scales (e.g., Commons et al. 1999, Aldrige et al. 2008).

The spatial distribution of highly suitable habitat for sage-grouse shifted as we expected in both spatial and environmental terms. The relatively low levels of overlap between the LBR model and both spring and winter models supports the idea that sage-grouse populations in this landscape migrate seasonally. Sage-grouse in our study region have previously been documented to used similar habitats during winter and breeding but move up to 80 km during summer following a gradient of green vegetation (Klebenow 1969, Connelly 1988). Sage-grouse use of a greater range of elevations during LBR probably reflects the sometimes slow movement up in elevation. Conservation efforts to preserve all seasonal components of sage-grouse habitat may be warranted if the goal is to maintain sage-grouse populations in the long term.

In contrast to sage-grouse, the distribution of pygmy rabbits was shaped by relatively finer scale variables likely reflecting the more restricted space use and possibly a greater degree of habitat specialization. As ranked by permutation importance, the top four variables in the pygmy rabbit model were calculated using habitat information at a fine scale (i.e., radii of ≤400 m), although a topographic position index (calculated using a 2-km radius) and proportion of land with >10% sagebrush cover at the broad-scale also were included. These results suggest that mapping pygmy rabbit distributions requires relatively fine-scale information. Another notable pattern of habitat selection for this species was reflected in observed occurrence over sagebrush covered areas at the broad-scale (5-km radius, Figure 2.3). Whereas all other response curves showed a positive relationship with the covariate, pygmy rabbits showed a peak around 60% of landscape with ≥10% sagebrush cover, and a decline at higher values. It is possible that pygmy rabbits either select for or are confined by other factors to habitat within 5 km of sagebrush edges. Although done at a finer spatial scale, previous research has indicated that pygmy rabbit habitat use has a positive relationship with distance from sagebrush edge (Pierce 2008).

Our species distribution and overlap estimates presented here are based on modeling processes with inherent biases that stem from both ecological and statistical assumptions. Balancing the degree of model fit to occurrence data is an issue in all modeling efforts and relatively well discussed in SDM (e.g., Radosavljevic and Anderson 2014). We used generally accepted best modeling practices to reduce sampling bias by spatial sub-sampling occurrence records, and by tuning model regularization multipliers (Hirzel et al. 2006, Merow et al. 2014, Searcy and Shaffer 2016). We also reduced the number of variables used in our models, although Maxent is robust to multiple variables, because AUC decreased only marginally as we reduced variables and literature suggests limiting complexity partly to help in model interpretation (Merow et al. 2014). Commission errors may be more common than usual in our pygmy rabbit models because of the patchy distribution of this species and the statistical assumption that a species is in equilibrium with the amount of suitable habitat available (Wiens et al. 2009). Using thresholds to create habitat suitability classifications also is a topic of debate (Merow et al. 2013, Liu et al. 2016), and our estimates of species overlap are influenced by our choices for threshold values.

Given that pygmy rabbits are correlated with habitat characteristics at fine scales, model performance might improve if we considered smaller neighborhoods than those suitable for wide-ranging sage-grouse. For example, occurrence of this species has long been understood to correlate with suitable soil characteristics, and it is likely that our soil variables (calculated using a 45 m radius) were not fine enough, neither thematically nor spatially, to be ranked higher in models. In addition, remotely sensed soil data are prone to error given the heterogenous distribution of soil types and properties, which is why we attempted to tease apart soil selection by this species using field sampling and site-level analyses.

As expected, the sage-grouse all-seasons model and the pygmy rabbit model, representing locations of each species recorded during any part of the year, exhibited a relatively high degree of overlap (Figure 2.4). The spatial distribution of overlap, however, was not consistent across the study region; sage-grouse high suitability habitat was more concentrated in the east and was generally less suitable and more fragmented farther west. This was not an apparent pattern in pygmy rabbit habitat (Figures 2.1). Overlap between sage-grouse and pygmy rabbits also varied across seasons, being highest during the LBR period and lowest during winter. Our analysis of the occurrence probability for each species showed that pygmy rabbits and sage-grouse occurred in the most similar areas of sagebrush cover and elevation during LBR, and all curves related to vegetation characteristics show the greatest disparity between sage-grouse and pygmy rabbits during winter (Figure 2.3). These results underscore the importance of evaluating species co-occurrence across temporal scales to design habitat conservation strategies at that benefit multiple species.

An important consideration in any co-occurrence study is the possibility of competition limiting the ability of two species to occupy the same area. We did not expect competition to be a driving factor influencing the negative co-occurrence of these species, however, we did not attempt to measure this. One resource these two species might compete for is the availability of highly palatable sagebrush (i.e., sagebrush with less monoterpenes and indigestible fibers), but there is no evidence, to our knowledge, that indicates this resource is limiting on landscapes where it is the primary vegetation type. It is more likely that sage-grouse and pygmy rabbits might compete for sagebrush cover in favored microhabitats such as mima mounds during sage-grouse nesting periods or for forage forbs during late brood-rearing periods when vegetation is desiccating. However, we are not aware of studies that have examined these possibilities.

We expected species overlap to decline at finer spatial and temporal scales, and a comparison with range-wide analyses of co-occurrence supports this expectation. Overlap between highly suitable habitat from the all-seasons model for sage-grouse and that for pygmy rabbits in our study region (49%) was lower than similar estimates at the geographic range scale (91%, Smith et al. *in review*). Overlap between highly suitable habitat for these species in our region also differed across seasons and was even less (18-30%), which emphasizes the need for incorporating appropriate spatial and temporal scales into conservation strategies that rely on species co-occurrence.

Appropriate umbrella species should represent the habitat needs of the community and especially other target species of conservation concern, and they should respond to ecosystem changes in ways that are predictable and similar to other target species (Andelman and Fagan 2000, Fleishman et al. 2000, Butler et al. 2012). Umbrella species often have similar habitat needs but more expansive use of space than the target species they protect (Sueter et al 2002). Sage-grouse obligate relationship with sagebrush, use of large landscapes and heterogenous areas, and sensitivity to anthropogenic disturbance make it an obvious choice for a system wide umbrella species. Sage-grouse may be better surrogates for other birds than for small mammals. Because birds occupy a diversity of habitats and represent a broad range of functional groups they are commonly included in conservation prioritization exercises (Larsen et al. 2012, Lentinti et al. 2015). For example, a large forest grouse, Capercaillie (*Tetrao urogallus*), acts as an umbrella species in the Swiss Prealps and study plots with these grouse have higher species richness and abundance of mountain birds of conservation concern than in those without Capercaillie (Sueter et al. 2002).

Because pygmy rabbits rely on soils that are suitable for burrowing, they use a narrower range of habitats and, in our study region, generally use smaller areas than sage-grouse. Consequently, pygmy rabbits might serve as a surrogate for other sagebrush species that also require friable soils conducive to hold burrow structure (e.g., sagebrush vole, *Lemmiscus curtatus*). Through their activities associated with burrowing, pygmy rabbits also serve as ecosystem engineers that influence many other species and processes, including sagebrush regeneration (Parsons 2016). Because conservation efforts may be most effective when they target key ecosystem engineers (Odling-Smee 2003), we suggest that land manager incorporate additional protection for pygmy rabbits, especially where pygmy rabbit habitat falls outside of areas used primarily by sage-grouse.

If long-term conservation of sage-grouse is a priority, then habitat management must recognize the heterogeneity of sagebrush landscapes and specific site characteristics conducive to sage-grouse survival during all parts of the annual cycle. Our results suggest that there is a decoupling of sage-grouse spring and LBR habitats in our study region, although winter habitat largely overlapped with spring habitat. Therefore, one possible simplification would be to focus conservation resources on spring and LBR habitat. This idea has been gaining traction, and some studies support this course of action (e.g., Aldridge and Brigham 2002, Donnelly et al. 2016).

Development of SDMs for regional populations of sage-grouse will be valuable as environmental and policy changes affect conservation and management in sagebrush systems. The availability of highly accurate species records (i.e., location information for specific individuals for which sex and age are known) can inform habitat selection and space use models to answer a diversity of questions related to habitat conservation for this species. While our models will likely be most useful to land managers and conservationists in east-central Idaho, they also demonstrate how species co-occurrence varies across space and time, with implications for habitat management aimed at multispecies conservation. When species of conservation concern are highly concentrated, land managers encounter fewer conflicts between habitat protection and other activities (Dobson et al. 1997). Limited availability of resources dedicated to land management and conservation often lead to simplified strategies for conservation goals (Sueter et al. 2002). Defining areas of high spatial overlap between species of conservation concern is a critical part of managing areas for multiple uses (Dobson et al. 1997, Andelman and Fagan 2000).

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Table. 2.1: Environmental variables used in sage-grouse and pygmy rabbit models, indicated by bullets. Variable codes are used as simplified titles for covariates in subsequent tables and figures. Scale refers to the area or neighborhood used to calculate the various metrics for a given 90-m pixel. The source information for each variable is also given.

TYPE	**VARIABLES**	**CODE**	**SAGE-GROUSE MODELS**				**PYGMY RABBIT**	**SCALE RADIUS (meters)**	**SOURCE; NOTES**
			Spring	**LBR**	**Winter**	**All-seasons**			
Land cover	Mean sagebrush cover (%)	sage	●	●	●	●	●	200	Provisional Remote Sensing Shrub/Grass NLCD Products (USGS 2016*a*, USGS 2017*a*); 2013 and 2014 source imagery
	Mean sagebrush height (cm)^1	sageht	●	●	●		●	200	
	Proportion of landscape in sagebrush with at least 10% cover	sage1k	●	●	●	●	●	1,000	
		sage5k	●	●	●	●	●	5,000	
	Mean tree canopy cover (%)	tree	●	●	●	●	●	200	NLCD 2011 USFS Tree Canopy (Analytical Version) (USGS 2016*b*)
	Proportion of landscape with > 3% forest canopy cover.	tree1k	●	●	●	●	●	1,000	
		tree5k	●	●	●	●	●	5,000	
	Proportion of agriculture (%)	ag	●	●	●	●	●	200	NLCD 2011 Land Cover (USGS 2014)
		ag1k	●	●	●	●	●	1,000	

	Proportion of landscape in agriculture	ag5k	●	●	●	●	●	5,000	
Topography	Mean elevation	elev	●	●	●	●	●	200	30-m Digital Elevation Model (USGS 2017*b*), Dilts (2015) [TPI]; TPI is the difference between elevation at a central point and the surrounding average elevation
	Terrain roughness; standard deviation of elevation	rough	●	●	●	●	●	200	
	Fine-scale Topographic Position Index (TPI), normalized	tpi500	●	●	●	●	●	500	
		tpi2000	●	●	●	●	●	2,000	
NDVI	Average NDVI during the LBR season (July1–Sep 22), calculated as the mean monthly maximums	NDVIave		●			●	125	Normalized Difference Vegetation Index (NDVI) (NASA 2015); an index to photosynthetic activity or vegetation greenness. Metrics were calculated annually, then averaged from 2000–2016.
	LBR intra-seasonal variability in NDVI, calculated as the standard deviation of monthly maximums	NDVIstd		●			●	125	
Soil	Soil available water capacity (m3/m3), averaged within the first 1 meter from the soil surface	awc					●	45	POLARIS soil data (Chaney et al. 2016).

	Soil bulk density (g/cm3), averaged within the first 1 meter.	bd					●	45	
	Percentage of calcium carbonate in soil, averaged within the first 1 meter	Caco3					●	45	
	Pore size distribution index (Brooks and Corey 1964).	lambda					●	45	
	Depth to restrictive layer (cm).	rstd					●	45	
	Percentage of sand in soil, averaged within the first 1 meter	sand					●	45	
	Percentage of silt in soil, averaged within the first 1 meter	silt					●	45	
Climate	19 bioclimatic variables patterned after Hijmans et al. (2005).	Bio1-Bio19					●	400	PRISM 30-year normals of precipitation and temperature (PRISM 2012).

Table 2.2: Thresholds used to classify pygmy rabbit and sage-grouse models into habitat suitability classes. Resulting percentage of locations (n) and area in each suitability class. For all sage-grouse models the low threshold balances, the moderate threshold is a value where the proportion of test observations is expected if observations were randomly distributed across habitat suitability values (F-ratio ≈ 1, calculated by the Boyce index; Hirzel et al. 2006), and the high threshold matches the mean predicted value of test observations. For the pygmy rabbit model, the low threshold matched the fixed cumulative value of 1 cloglog threshold as calculated by maxent, the moderate threshold is the value that maximizes test sensitivity plus specificity, and the high threshold is a value that achieved an F-ratio of 3.5 as calculated by the Boyce index and was close to sage-grouse thresholds.

Model (n)	**Habitat Suitability**	**Threshold**	**Proportion of Locations**	**Area (km^2)**
Spring (18,620)	Non-habitat		1%	9,423
	Low	0.08	12%	5,640
	Moderate	0.40	26%	3,502
	High	0.66	61%	3,191
LBR (10,123)	Non-habitat		1%	9,555
	Low	0.09	12%	5,612
	Moderate	0.32	28%	4,083
	High	0.65	59%	2,505
Winter (5,474)	Non-habitat		2%	12,107
	Low	0.04	14%	5,878
	Moderate	0.37	22%	2,250
	High	0.67	62%	1,521
All-seasons (20,069)	Non-habitat		1%	8,403
	Low	0.09	13%	5,840
	Moderate	0.41	24%	3,556
	High	0.65	62%	3,957
Pygmy rabbit (248)	Non-habitat		1%	8,866
	Low	0.04	9%	7,084
	Moderate	0.35	35%	3,503
	High	0.64	56%	2,303

Table 2.3: Final model variables per species and season where applicable, with variable importance indicated by percent contribution and permutation importance.

Environmental Variables	**Species and Season (percent contribution, permutation importance)**				
	Sage-grouse				**Pygmy Rabbit**
	Spring	**LBR**	**Winter**	**All-seasons**	
Mean Sagebrush Cover (%)					4.1, 9.7
Mean sagebrush height (cm)	15.4, 9.8	16.6, 5.7	3.1, 2.3		
Mean Tree Canopy Cover (%)					22, 6.6
Proportion of Agriculture (%)			12.5, 8		
Proportion of landscape in sagebrush with at least 10% cover (1 km radius)	6.6, 5.7	31.9, 5.6		9.2, 6.2	
Proportion of landscape in sagebrush with at least 10% cover (5 km radius)			6.1, 6.9		0.7, 2.6
Proportion of landscape with > 3% forest canopy cover (1 km radius)	61, 45.6	14.7, 32.6	62.3, 39.7	51, 43.9	
Proportion of landscape in agriculture (5 km radius)	6.6., 10.2	4.3, 9.7	4, 12	19.6, 14.1	
Mean Elevation	0.6, 2.9	2.7, 3	1.3, 6.9	3.9, 3.6	
Terrain Roughness; standard deviation of elevation	5.3, 12.4	21, 26.5	6.7, 12.5	12.9, 23.2	28.9, 34.9
Fine Scale Topographic Position Index (500 m radius)	1.5, 4		1.1, 3.7		
Broad Scale Topographic Position Index (2 km radius)	2.9, 9.5	1.8, 4.4	2.8, 8	3.5, 9.1	5.2, 7.5
Average NDVI During LBR Season		1.5, 4.3			12.8, 10.5
Standard Deviation of NDVI in LBR Season		5.7, 8.4			
Pore size distribution index (Brooks and Corey 1964).					2.2, 4.2
Percentage of silt in soil, averaged within the first 1 meter from the soil surface.					4.6, 9
Temperature of the Warmest Quarter of the Year					19.1, 12.4
Temperature of the Coldest Quarter of the Year					0.4, 2.6

Table 2.4: Overlap of highly suitable habitat for seasonal and general sage-grouse models. For percentages, the total area of highly suitable habitat (in the column heading) is divided by the area of high suitability habitat overlap between model types (in the cell). All areas are in km^2.

Model	**Spring (3,191 km^2)**	**LBR (2,505 km^2)**	**Winter (1,521 km^2)**	**All Seasons (3,957 km^2)**	**Pygmy Rabbit (2,303 km^2)**
Spring		53% (1,329)	67% (1,026)	73% (2,883)	31% (704)
LBR	42% (1,329)		5% (72)	46% (1,807)	31% (712)
Winter	32% (1,026)	3% (72)		31% (1,221)	18% (422)
All Seasons	90% (2,883)	72% (1,807)	80% (1,221)		49% (1,129)
Pygmy Rabbit	22% (704)	28% (712)	28% (422)	29% (1,129)	

Table 2.5: Correlation between models of habitat for sage-grouse (SG) and pygmy rabbits in east-central Idaho. Pearson's correlation (r) is based on 1,000 random sample points (p <0.0001 for all r). Two common overlap statistics, Schoener's D (Schoener 1968) and the I statistic (Warren et al. 2008).

Models	**Spring (SG)**	**LBR (SG)**	**Winter (SG)**	**All Seasons (SG)**	**Pygmy Rabbit**
Spring (SG)		r = 0.749	r = 0.783	r = 0.960	r = 0.582
LBR (SG)	D = 0.748 I = 0.943		r = 0.356	r = 0.811	r = 0.600
Winter (SG)	D = 0.704 I = 0.929	D = 0.512 I = 0.803		r = 0.739	r = 0.449
All Seasons (SG)	D = 0.898 I = 0.989	D = 0.781 I = 0.957	D = 0.668 I = 0.908		r = 0.685
Pygmy Rabbit	D = 0.656 I = 0.882	D = 0.665 I = 0.894	D = 0.530 I = 0.795	D = 0.701 I = 0.912	

Figure 2.1: The classified all-seasons sage-grouse model (a) and pygmy rabbit model (b). Variables used are detailed in Table 2.1 and threshold values in Table 2.2.

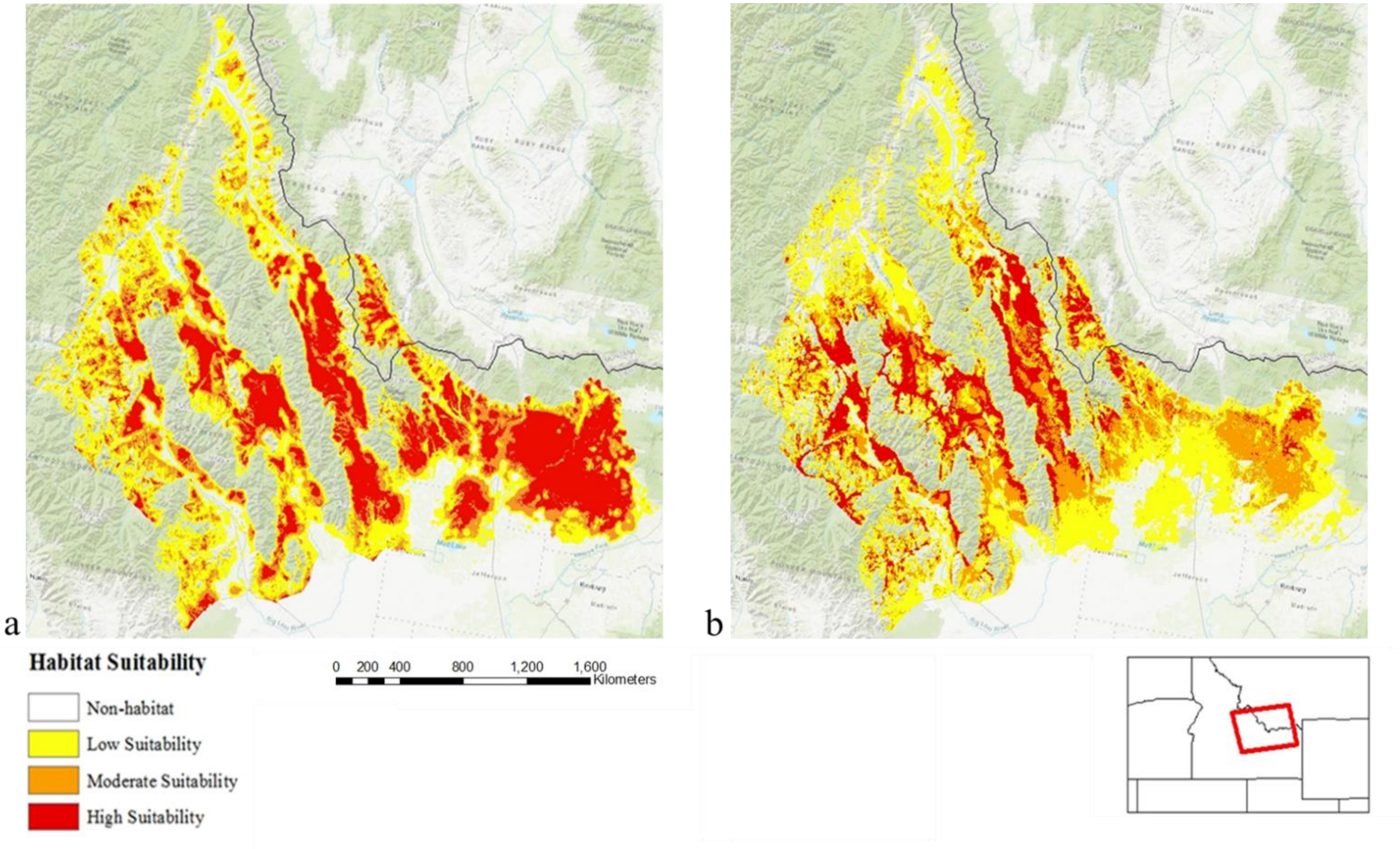


Figure 2.2: Three seasonal models for sage-grouse within our study area: (a) Spring (March 1 – June 30), (b) Late Brood-rearing habitat for hens (July 1 – Sep 22), and (c) Winter (Dec 1 – Feb 29). Additional model details can be found in 2.1, 2.2., and 2.3.

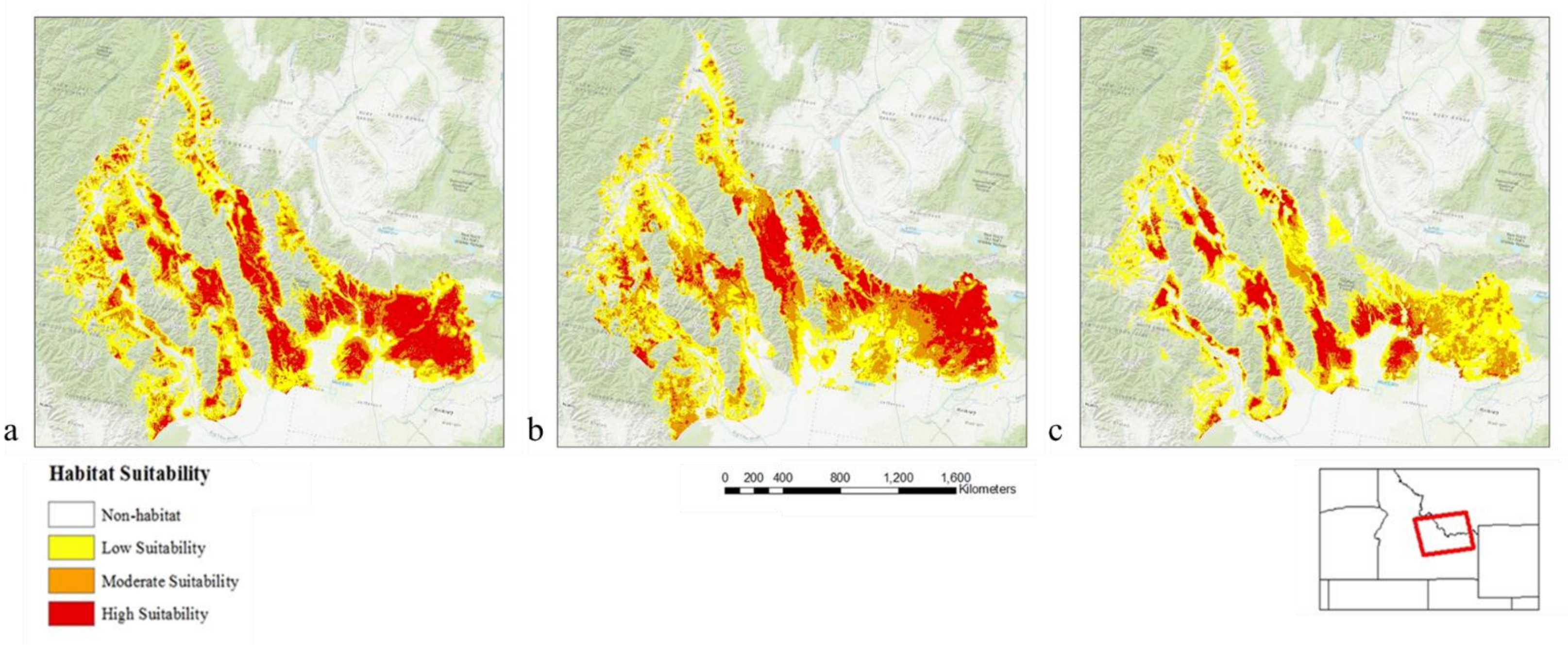


Figure 2.3: Percent of occurrence locations along nine different environmental gradients. Lines represent smoothed trends for these relationships using the “loess” method in ggplot2 (Wickham 2016).

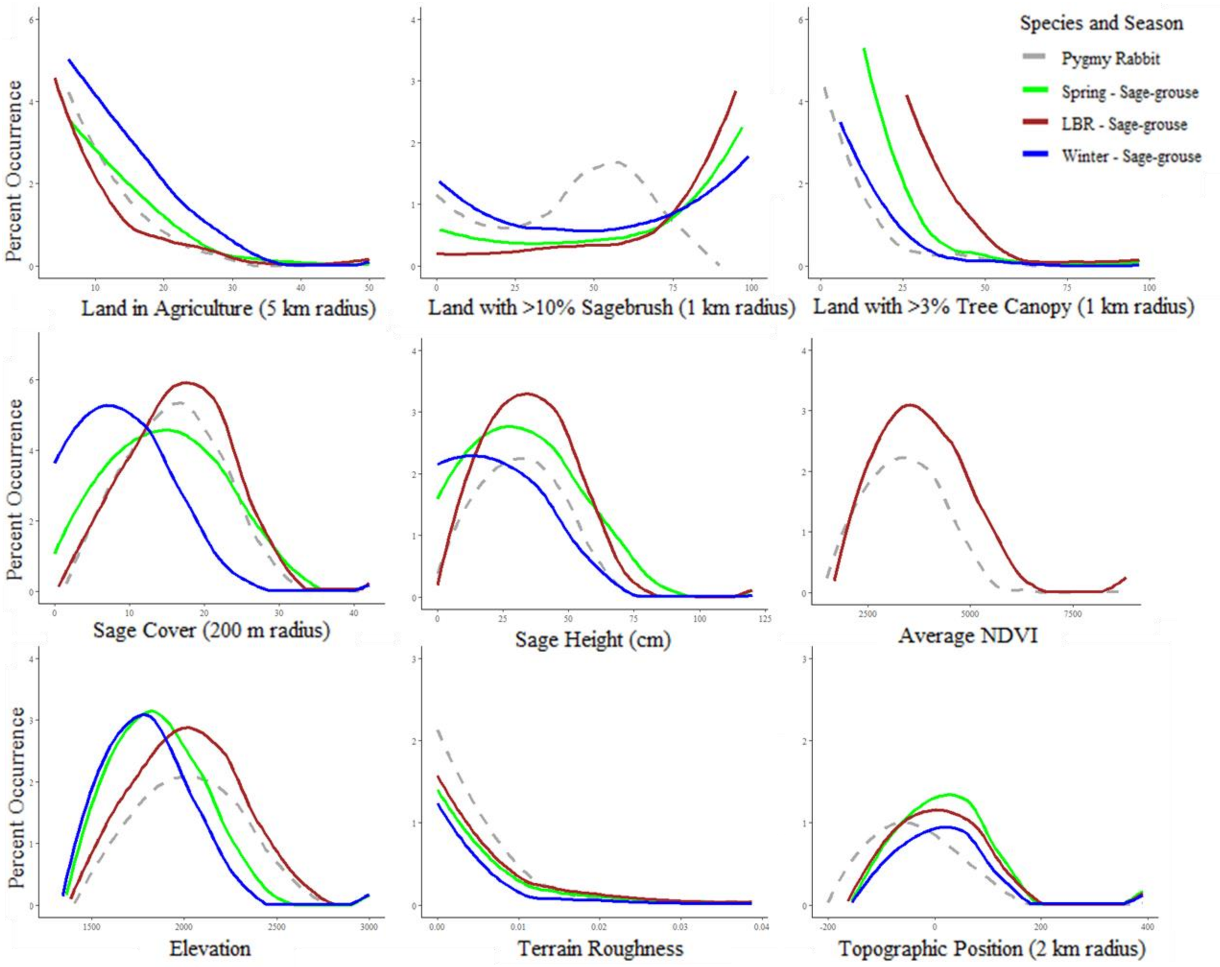


Figure 2.4: Venn diagrams illustrating the amount of high-quality habitat for sage-grouse in each season, the amount of high-quality habitat for pygmy rabbits, and the amount which these habitats overlap.

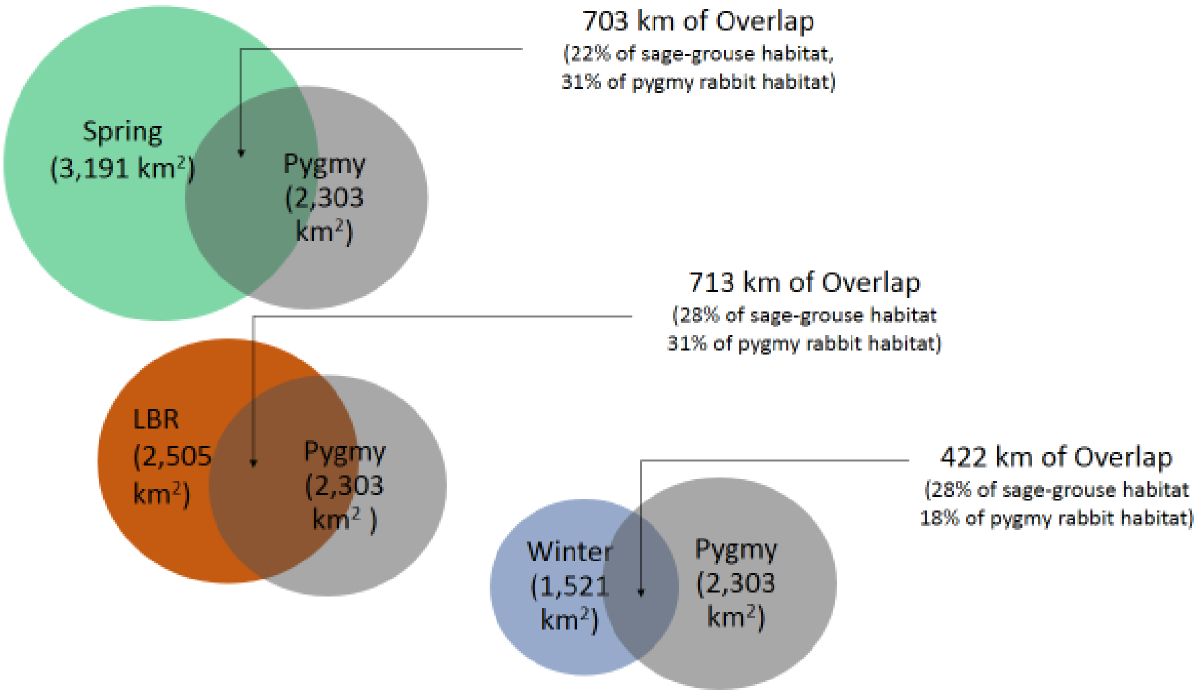
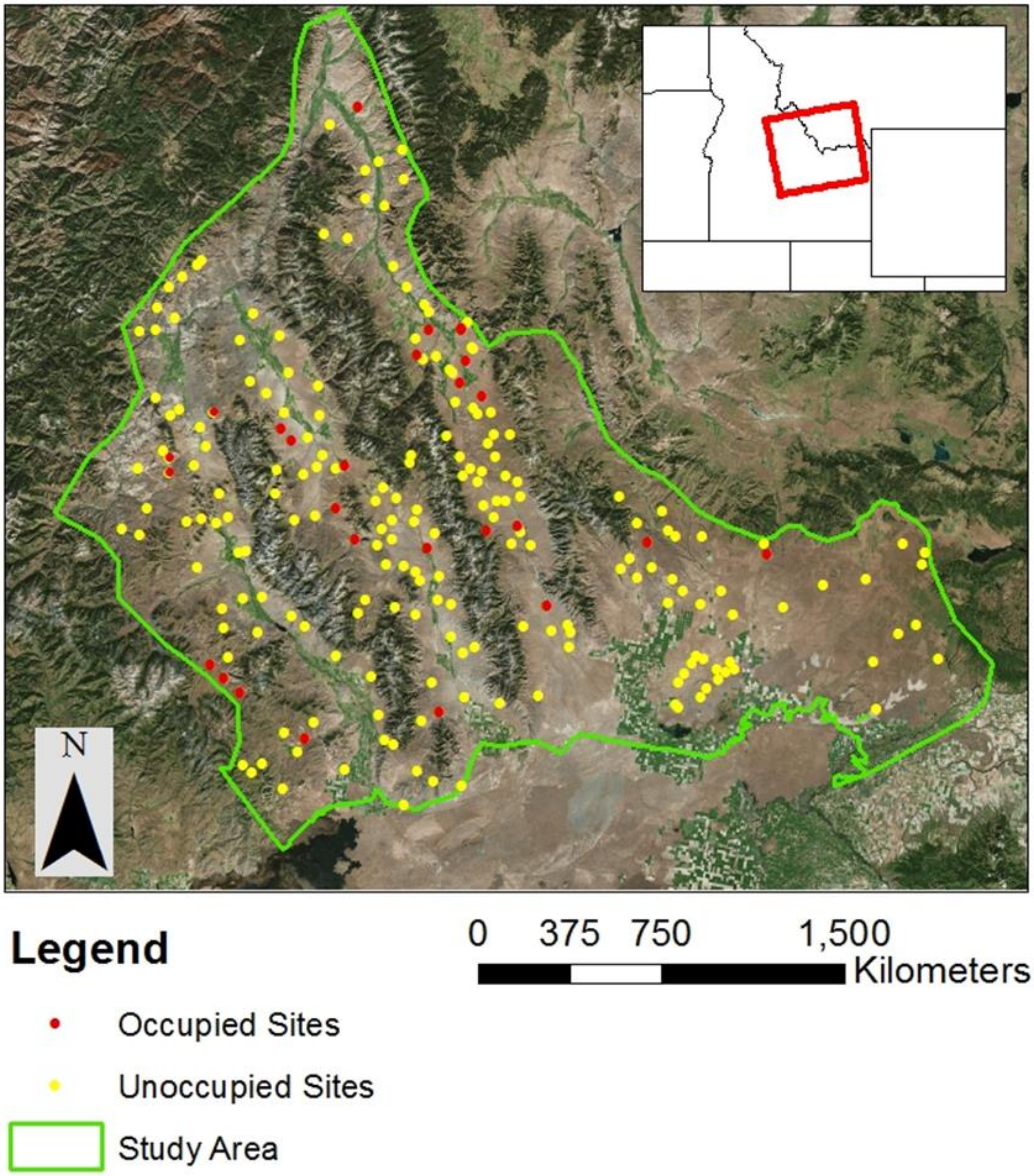


Figure 2.5. Sites surveyed for presence of pygmy rabbits, vegetation and soil characteristics in east-central Idaho during 2018.



General Conclusion

Our work provides an analysis of species overlap between two habitat specialists viewed through the lens of the umbrella species strategy. We documented that sage-grouse distribution and the distribution of lands designated for sage-grouse conservation overlap highly with pygmy rabbits at broad geographic extents. At finer spatial and temporal scales, however, overlap between the species was reduced and variable. This research illustrates how the scale at which ecological studies are conducted can influence the results and conclusions reached, and it demonstrates how observed co-occurrence between species can decrease as spatiotemporal scale becomes more precise. Despite their obligate relationship with sagebrush shrubs, differences in the distributions of these two habitat specialists warrant further attention if long term persistence of both species is a management goal. Additionally, we provide tools that can inform conservation efforts for pygmy rabbits in the form of distribution models.

At the broad scale of sage-grouse conservation in the western US and the pygmy rabbit geographic range, sage-grouse HMAs overlapped highly with areas occupied by, and predicted to by high suability habitat for, pygmy rabbits. Umbrella species are chosen when they require large areas that overlap with other species of concern or help prioritize habitat remnants for conservation, making sage-grouse an obvious choice for the sagebrush steppe given their distribution in this system (Wilcox 1984; Noss 1990; Fleishman et al. 2000). Our results support the current prioritization of HMAs for pygmy rabbit conservation; PHMAs encompass 59% and GHMAs encompass of 34% of primary habitat for pygmy rabbits. The sage-grouse HMA umbrella strategy does encapsulate a large amount of primary pygmy rabbit habitat (i.e., 91%), but pygmy rabbit occupied areas and suitable habitat patches outside of HMAs may need additional conservation attention.

At regional and refined temporal scales, overlap between sage-grouse and pygmy rabbits was considerably less than at broad extents. Of pygmy rabbit habitat, 49% of highly suitable habitat at the regional scale and 91% of primary habitat at the geographic range scale for pygmy rabbits overlaps with highly suitable habitat for sage-grouse. Our regional study may have more significant and better tailored results to co-occurrence between these species at a scale relevant to land management projects. Projects such as oil and gas lease sales and sagebrush thinning treatments usually are evaluated and conducted at a scale closer to our regional study extent (Pierce et al. 2010, Wilson et al. 2010, Germaine et al. 2017). When considering the impacts that these projects might have on wildlife, it is useful to know that a simple evaluation of the potential effects on habitat quality for sage-grouse might not represent the effects on other wildlife, even other sage-brush obligates like the pygmy rabbit. At sites scales, it may be necessary to conduct surveys for pygmy rabbits before projects are implemented that would disturb soils or sagebrush shrubs.

Our study illustrates how analyses of ecological phenomena at different scales can lead to different conclusions. Even though we used fine resolutions for the habitat model for pygmy rabbits at the geographic range scale (i.e., 30 x 30 m pixels), the range of habitats predicted to be highly suitable for this species was much larger when analyzed at this broad extent than when analyzed at a regional extent. A visual comparison of both pygmy rabbit model predictions revealed that the highly suitable habitat category at the geographic range scale encapsulated both moderate and high suitability habitat at the regional scale (i.e., our classification of high suitability habitat resulted in less area at the regional scale). This is likely because our geographic range model had a higher number of occupied locations that were spread across a larger range of environments (i.e., 10,420 locations across ~1 million km^2 at the geographic range scale and 428 locations across ~20,000 km^2 at the regional scale). Therefore, at a broad spatial scale, the constraints limiting pygmy rabbit distribution seem to be less stringent, from a modeling perspective, and more environments and space are predicted to be within the limits of this species habitat. At the regional scale, however, a smaller modeling extent reduced the diversity of environments represented in the occurrence locations, which would have allowed the program to calculate a more refined set of constraints.

Pygmy rabbits are a unique species, and one with potential to garner public support for sagebrush conservation, yet the future of this species is far from certain. As research and surveying for this species continues, our estimates of minimum area occupied and predictions from our species distribution models can be updated with new occurrence data and new environmental information. With range contractions and regional extirpations predicted for this species (Leach et al. 2015), a better understanding of species trends in the four major habitat regions we identified across time is needed if land managers are to succeed in conserving this species. Additionally, pygmy rabbits could be considered the mammalian equivalent of sage-grouse, given their obligate association with sagebrush. This coupled with a sensitivity and negative response to sagebrush disturbance could make pygmy rabbits another species that is considered in surrogate species strategies (Pierce et al. 2010, Wilson et al. 2010, Germaine et al. 2017). Conservation umbrellas and strategies designed to meet the needs of multiple species across multiple scales will likely benefit long-term maintenance of biodiversity and resilience of the sagebrush ecosystem.

Appendix A:

Pygmy Rabbit Geographic Range Model Covariates

Information about all environmental variables considered in distribution modeling for pygmy rabbits spatial resolution, year published, and description of data processing.

Theme	Environmental Variable	Resolution & Year	Description of Data & Processing steps
Topography	Aspect [a]	30m, 2013	The compass direction of a slope’s face.
	Curvature[a]	30m, 2013	Using Elevation layer, calculated curvature using spatial analyst tool, calculates the curvature of a raster surface.
	Elevation	30m, 2013	Digital elevation model.
	Slope[a]	30m, 2013	Slope steepness in degrees.
Soils	Available Water Capacity[b]	3 arcsec (~100m), 2016	Soil available water capacity (m^3/m^3), averaged within the first 1 meter from the soil surface.
	Bulk Density[b]	3 arcsec (~100m), 2016	Soil bulk density (g/cm^3), averaged within the first 1 meter from the soil surface.
	Calcium Carbonate Percentage[b]	3 arcsec (~100m), 2016	Percentage of calcium carbonate in soil, averaged within the first 1 meter from the soil surface.
	Clay Percentage[b]	3arcsec (~100m), 2016	Percentage of clay in soil, averaged within the first 1 meter from the soil surface.
	Pore Size Distribution[b]	3arcsec (~100m), 2016	Pore size distribution index (Brooks and Corey 1964).
	Restrictive Layer Depth[b]	3arcsec (~100m), 2016	Depth to restrictive layer (cm).
	Sand Percentage[b]	3arcsec (~100m), 2016	Percentage of sand in soil, averaged within the first 1 meter from the soil surface.
	Silt Percentage[b]	3arcsec (~100m), 2016	Percentage of silt in soil, averaged within the first 1 meter from the soil surface.
Vegetation	Time Integrated NDVI [c]	250m, 2015	Canopy photosynthetic activity across the entire growing season. Average daily (interpolated) integration of NDVI above the baseline for the entire duration of the growing season from 2001 to 2015.
	Big Sagebrush[d, e]	30m, 2011	Amount of area mapped as big sagebrush. Includes ecological systems with at least two *Artemsia tridentata* ecosystem components according to Natureserve Explorer (Level 3 codes 5205, 5705, 5706, 5307, 5308, and 5704). Grid cells with these codes were assigned a value of 1 and all other cells a 0. The sum in a 3x3 (90m x 90m) neighborhood was assigned to the cell.

	Herbaceous Cover[a]	30m, 2016	Percent herbaceous cover. Reclassified Existing Vegetation Cover data to only include herb categories, the rest classified as “no data”. Cells within a 3x3 (90 m x 90 m) neighborhood were used to calculate the majority value for each cell.
	Shrub Cover[a]	30m, 2016	Percent shrub canopy cover. Reclassified Vegetation Cover data to only include shrub categories, the rest classified as “no data”. Cells within a 3x3 (90 m x 90 m) neighborhood were used to calculate the majority value for each cell.
	Shrub Height Majority[a]	30m, 2016	Majority shrub height. Reclassified Vegetation Height data to include only shrub height. Bins were assigned their median value and then the majority value within a 3x3 (90 m x 90 m) neighborhood was assigned to the cell.
	Shrub Height Maximum[a]	30m, 2016	Maximum shrub height. Reclassified Vegetation Height data to include only shrub height. Bins were assigned their median value and then the maximum value within a 3x3 (90 m x 90 m) neighborhood was assigned to the cell.
Climate	Bio 1 -19 (19 variables) [f]	800 m, 2010	The annual values for 30-year normals of precipitation and temperature were used to calculate 19 bioclimatic variables patterned after Hijmans et al. (2005).
Fire	Fire Regime [a]	30m, 2010	Characterization of the presumed historical fire regimes. Cells within a 3x3 (90 m x 90 m) neighborhood were used to calculate the majority value for each cell.
	Mean Fire Return Interval[a]	30m, 2016	Average period between fires under the presumed historical fire regime, categorized into ranges of years (26 classes). Cells within a 3x3 (90 m x 90 m) neighborhood were used to calculate the majority value for each cell.

[a] Landfire: (USGS 2016) https://www.landfire.gov/index.php

[b] Polaris: (Chaney et al. 2016) http://stream.princeton.edu/POLARIS/

[c] USGS Remote Sensing Phenology (USGS 2018c): https://phenology.cr.usgs.gov/get_data_250w.php

[d] USGS GAP Land Cover Data Portal: (USGS GAP 2016) https://gapanalysis.usgs.gov/gaplandcover/data/

[e] Natureserve Explorer: (Natureserve 2018) http://explorer.natureserve.org/index.htm

[f] PRISM: (PRISM 2012) www.prism.oregonstate.edu/normals/

Appendix B:

Pygmy Rabbit Geographic Range Model Details for All Extents and Structures

Statistics for comparing model performance as extent, number of variables, and regularization multiplier were varied. Area under the curve (AUC) and Akaike Information Criterion (AIC) values, as well as a visual inspection of the predictive map output, were used to select the number of variables and the regularization multiplier (L1) in our final model. Each model was replicated 5 times, and values are averaged over the 5 replicates.

Model Extent (L1 regularization multiplier used)	Regularization Multiplier	# of Variables	Mean Test AUC	Mean Delta AIC within extent
Full 10km	1	39	0.768	0
Reduced 10km	1	18	0.767	214.82
Reduced 10km	5	18	0.743	1323.19
Reduced 10km	10	18	0.712	1743.01
Full 50km	1	39	0.856	0
Reduced 50km	1	18	0.848	393.56
Reduced 50km	5	18	0.836	1197.5
Reduced 50km	10	18	0.832	1196.6
Full range	1	39	0.889	0
Reduced range	1	17	0.885	290.64
Reduced range	5	17	0.876	962.53
Reduced range	10	17	0.875	962.44

Appendix C:

Pygmy Rabbit Geographic Range Final Model Thresholds

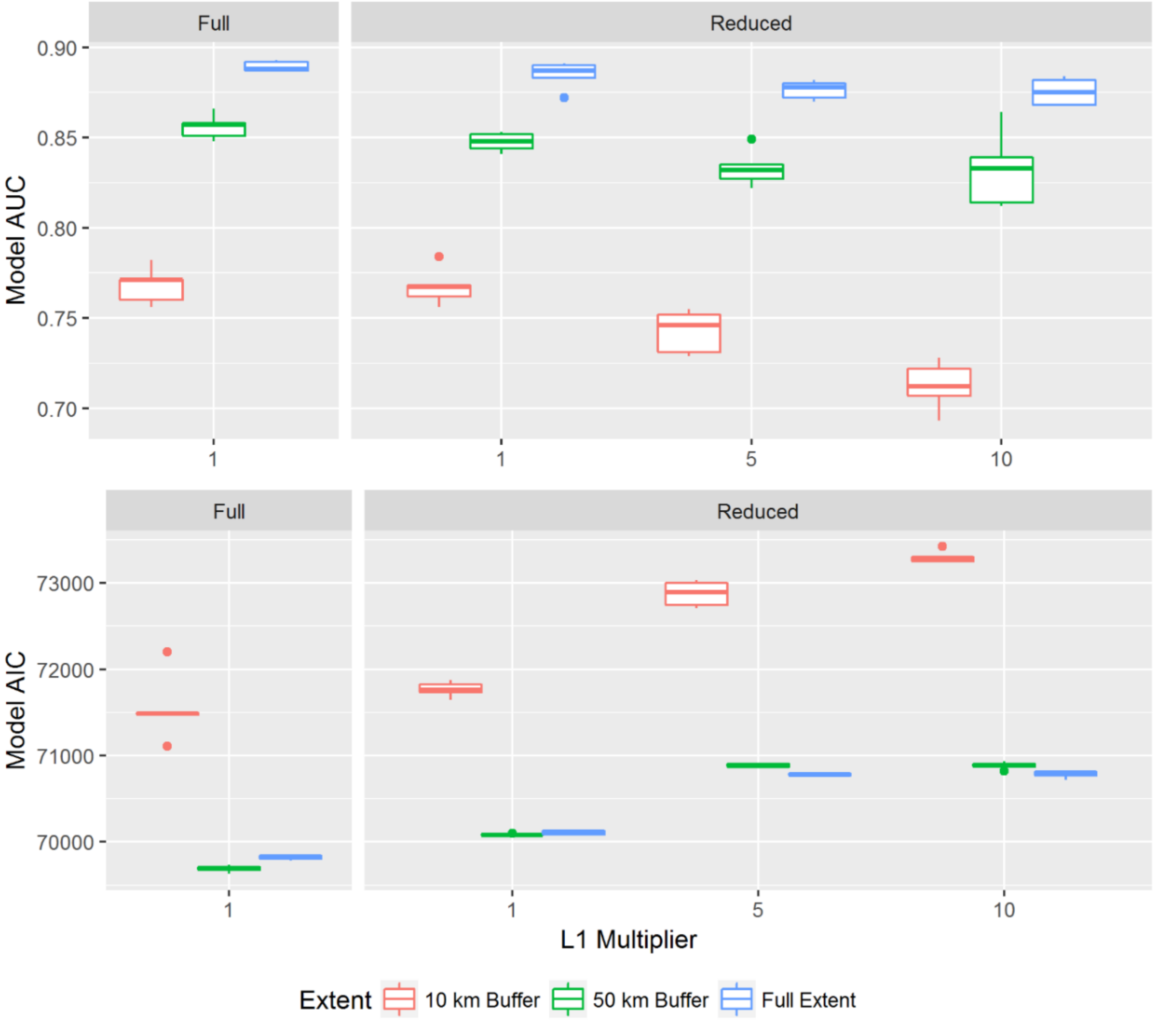
Maxent modeled thresholds used in aiding interpretation of habitat suitability. Threshold values used for characterizing suitability of habitat for pygmy rabbits are marked with an asterisk (*).

Threshold	Cloglog threshold for final model	Percent of study area above threshold	Training omission	Test omission	Binomial probability
Minimum Training presence	0.0060	77.89	0	0.0017	0
Fixed cumulative value 1	0.0333	58.37	0.0031	0.0039	0
Balance training omission, predicted area, and threshold value	0.0815	46.58	0.0101	0.0144	0
Fixed cumulative value 5	0.1361	39.54	0.0308	0.0337	0
Equate entropy of threshold and original distributions	0.1723	36.25	0.0439	0.0448	0
Fixed Cumulative value 10	0.2486	30.87	0.0727	0.0768	0
10 percentile training presence	0.3038	27.82	0.0995	0.1033	0
Maximum test sensitivity plus specificity*	0.3167	27.16	0.1070	0.1006	0
Maximum training sensitivity and specificity	0.3265	26.66	0.1064	0.1161	0
Equal test sensitivity and specificity*	0.4661	20.39	0.1986	0.204	0
Equal training sensitivity and specificity	0.4705	20.21	02019	0.2078	0

Appendix D:

Pygmy Rabbit Geographic Range Model AUC and AIC for All Extents and Structures

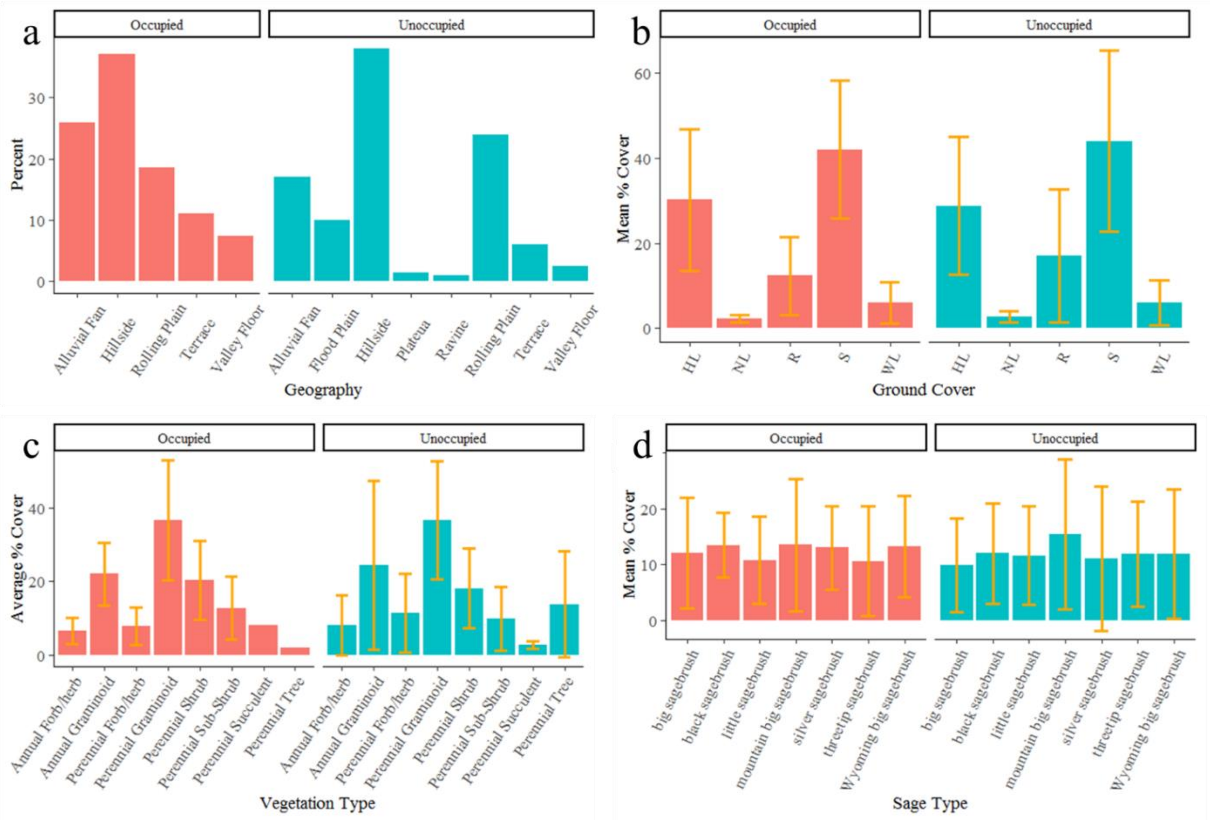
Boxplots of testing AUC and AIC for 5 replicates of each model used to guide selection of structure, extent, and L1 regularization multiplier for our final model.



Appendix E:

Site Level Averages

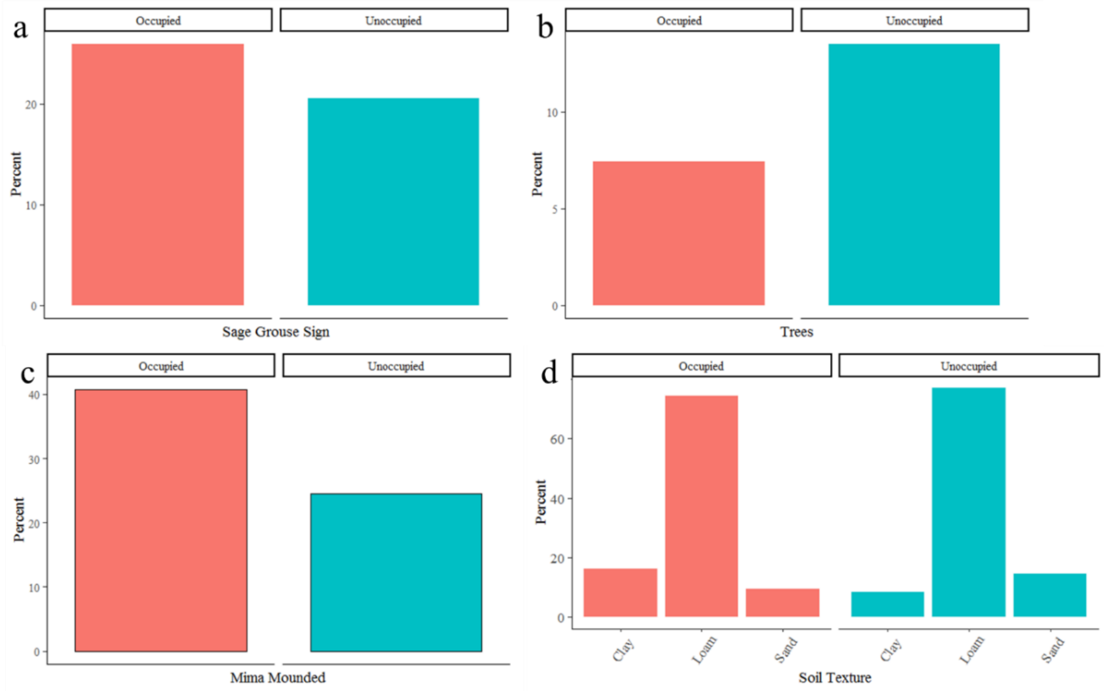
(a) Percentage of non-occupied sites and occupied site locations characterized by eight different observed geographic feature types. (b) Average percent of ground cover type found at occupied and unoccupied sites. (c) Mean cover percentage of all vegetation growth forms and duration types for both occupied and unoccupied sites. (d) Mean percent cover of sagebrush types in occupied and unoccupied sites for sites with sagebrush species present.



Appendix F:

Site Level Observations

Percentage of sites with observed characteristics grouped by occupancy status.



Appendix G:

Soil Textures

Percent of soil textures in a given soil horizon found at occupied and unoccupied sites.