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Overlap Between Sagebrush Habitat Specialists Differs Among Seasons: Implications for Umbrella Species Conservation ☆,☆☆

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ABSTRACT

Conservation strategies that rely on umbrella species depend on spatial overlap with target species of concern, yet the temporal and spatial scale at which co-occurrence is assessed is rarely considered. In seasonal environments, shifts in space use across seasons could alter patterns of co-occurrence, especially at regional and local scales that are relevant to land management. Greater sage-grouse *(Centrocercus urophasianus),* which currently serve as an umbrella species for sagebrush ecosystems across the western United States, move between seasonal habitats. Our goal was to evaluate the degree to which sage-grouse general and seasonal habitats overlap with habitat for another sagebrush-dependent species of conservation concern, the pygmy rabbit *(Brachylagus idahoensis).* We created inductive species distribution models for both species in east-central Idaho. We used maximum entropy methods to build models incorporating environmental factors representing topography, vegetation, climate, and soil characteristics. Despite both species being sagebrush obligates, we documented a relatively modest degree of spatial overlap between these species across the region; only 49% of highly suitable habitat for pygmy rabbits overlapped with areas mapped as highly suitable for sage-grouse when considering general habitat, and overlap was lower (18–31%) when we evaluated seasonal sage-grouse distributions. Our models predicted that pygmy rabbits would also occur in narrow (1–2 km) sagebrush corridors between steep terrain features where sage-grouse are typically absent. This work suggests that additional habitat conservation for pygmy rabbits will be needed to support their long-term persistence, especially where their habitat falls outside of areas designated as primary habitat for sage-grouse. Our models provide useful information for land management and habitat restoration within the study region and also offer a cautionary tale for application of simplified conservation strategies like the designation of umbrella species. Incorporating spatial and temporal scales into assessments of co-occurrence may increase effectiveness of conservation strategies involving surrogate species.

Introduction

Surrogate species strategies are frequently used to streamline conservation actions at broad extents because limited resources are available to study the habitat requirements of all species throughout an ecosystem. Umbrella species are 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 for each species (Caro and O'Doherty 1999; Roberge and Angelstam 2004). The umbrella species approach assumes that a management action for one species will similarly affect others, but it only works when there is significant overlap in habitat selection and space use. Models of habitat similarity or species distribution maps are typically used to evaluate overlap

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(Caro 2003; Roberge and Angelstam 2004; Rowland et al. 2006), although seasonal overlap is rarely considered.

Variation in temporal patterns of space and habitat use is common in seasonal environments, and behaviors such as migration have evolved in response to seasonal changes in resource quality and availability (Hutchison and Maness 1979; Bradshaw and Holzapfel 2007). Although longer temporal scales (i.e., successional and climatic periods) have been addressed in the species distribution 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 species (Lindenmayer et al. 2002; Favreau et al. 2006).

In this study we examined predicted habitat overlap of two sagebrush obligates 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 US history (Division of Public 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). Previous studies have quantified spatial overlap between sage-grouse and mule deer (*Odocoileus hemionus;* Copeland et al. 2014), songbirds (Hanser and Knick 2011; Barlow et al. 2019; Timmer et al. 2019), reptiles (Pilliod et al. 2020), and suites of multiple species (Rowland et al. 2006; Carlisle et al. 2018; Runge et al. 2019). Many of the target species in these studies exhibited moderate to high levels of overlap with sage-grouse habitat or conservation areas or were believed by the authors to benefit to some degree from habitat conservation aimed at sage-grouse (except sagebrush sparrows, *Artemisiospiza nevadensis,* Thimmer et al. 2019). However, several authors noted that the benefits were due, at least in part, to the large range of areas used by sage-grouse (Hanser and Knick 2011) and that microhabitat associations for other species should be considered (Barlow et al. 2019). Like sage-grouse, the pygmy rabbit is a sagebrush-obligate currently designated as vulnerable, imperiled, or critically imperiled in all 9 range states (NatureServe 2020). While both species have been petitioned for threatened status under the Endangered Species Act (Federal Register 2004, 2010), conservation efforts to date have focused on conserving habitat for sage-grouse with the expectation that habitat for pygmy rabbits and other sagebrush-associated species would be protected under a sage-grouse umbrella.

Many aspects of sage-grouse and pygmy rabbit 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). Sagebrush also provides structural 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 (Dalke et al. 1963; Connelly et al. 1991, 2000; Donnelly et al. 2016). 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 concealment for their nests, as well as forage (Connelly et al. 1991; DeLong et al. 1995; Connelly et al. 2000; Coates and Delehanty 2010). Female sage-grouse rear their broods for at least 2–3 wk in the vicinity of their nest before moving to summer range, using sagebrush habitat with a healthy herbaceous understory and abundant insects critical to the survival of young chicks (Connelly et al. 2016). The beginning of the late brood-rearing (LBR) season during the summer coincides with a shift in diet from predominantly insects to forbs (Klebenow and Gray 1968). During this season habitat selection is driven by forb availability, and sage-grouse follow phenological shifts in vegetation to feed on succulent forbs, moving to either higher-elevation sites or mesic habitats adjacent to sagebrush with abundant forbs, including agricultural lands, wet meadows, and riparian areas (Drut et al. 1994; Connelly et al. 2016 Donnelly et al. 2016). 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). In winter, sage-grouse diet is composed almost exclusively of sagebrush leaves, which must be accessed above the snow if present. Research in Idaho documented that sage-grouse preferred black sagebrush *(A. nova)* during winter where it is available; although relatively low-growing, black sagebrush have relatively lower levels of monoterpenes and therefore are more palatable than other varieties (Frye et al. 2013). Where black sagebrush is not available, sage-grouse tend to use areas of relatively dense (> 10% cover) and tall (> 20 cm) sagebrush (Braun et al. 2005; Frye et al. 2013). Slope and aspect influence 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. Pygmy rabbits use relatively dense and tall sagebrush communities with soil characteristics that are conducive to burrowing, such as the presence of deep, loamy soils. Populations are often associated with features such as alluvial fans, drainages, and microtopography (e.g., mima mounds) that foster relatively deep soils (Grinnell et al. 1930; Borell and Ellis 1934; Weiss and Verts 1984; McMahon et al. 2017). Although some juveniles exhibit relatively long-distance natal dispersal movements (Estes-Zumpf and Rachlow 2009), adults appear to remain within home ranges once established. Reported estimates of annual home ranges vary from 4 to > 12 ha, with males using larger areas during the breeding season than at other times of year (Sanchez and Rachlow 2008).

The goal of this study was to estimate regional distributions for both pygmy rabbits and sage-grouse in east-central Idaho and evaluate general and seasonal (spring, LBR, and winter) patterns of spatial overlap between species. We selected sage-grouse seasons that are emphasized in management: spring for lekking, nesting, and early brood-rearing activities; LBR, specifically pertaining to the needs of female sage-grouse and their broods for population recruitment; and winter, which is important to annual survival and when sage-grouse often use discrete habitat. Fall and male summer distributions are not a management focus but are incorporated into a general sage-grouse distribution model.

We hypothesized that (H1) all sage-grouse distributions would be positively associated with sagebrush cover, the amount of sagebrush in the landscape, and a lack of tree canopy cover and agriculture. Because habitat transitions depend on annual conditions, we expected significant seasonal overlap. However, we predicted that LBR habitat used by female sage-grouse would also include higher elevations and more varied habitats with green vegetation (i.e., higher vegetative productivity) during late summer. In winter, we expected distributions to be tied to sagebrush communities with relatively short sagebrush compared to other seasons and shift to lower elevations. For pygmy rabbits, we hypothesized that (H2) distribution would strongly reflect vegetation and soil properties at fine scales. We predicted that pygmy rabbit habitat would be characterized by increased sagebrush

cover and height, and soils that have loamy textures and medium porosities.

Across the full extent of the pygmy rabbit range, 91% of modeled habitat fell within sage-grouse range (Smith et al. 2019). However, we expected that this pattern would differ at a regional extent, where distributions would be tuned to local environmental conditions and not averaged across the species' range. We hypothesized that at the smaller, regional extent of this study, (H3) the two species would still exhibit a high degree of overlap because of their dependence on sagebrush-dominated habitats, but overlap would be less than at range-wide extents. Further, we expected that (H4) the degree of spatial overlap 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 both species use areas of abundant, tall sagebrush with a productive herbaceous cover for nesting and early brood-rearing (sage-grouse) and forage (pygmy rabbit).

We provide an evaluation of the spatial overlap of two highly specialized sagebrush obligate species and demonstrate how putatively similar habitat needs can vary in time and space. The spatial distribution models (SDMs) and analyses of overlap can inform conservation strategies for sagebrush communities at regional scales that are relevant to many habitat management, restoration, and conservation planning decisions.

Methods

Study area

We focused our regional analysis where both pygmy rabbits and sage-grouse occur in east-central Idaho, along the border with Montana, an area that is defined by basin and range topography, including multiple mountain ranges (Fig. 1, inset). This region (21 756 km^2) was adapted from the Mountain Valleys Conservation Area for sage-grouse identified in the approved resource management plan amendment published by the Bureau of Land Management (BLM) in Idaho (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 (2 700–3 000 m), 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 three-tip sagebrush *(A. tripartita)* are common foundation species in these areas, as well as rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.). Invasive graminoids like cheatgrass *(Bromus tectorum)* and medusahead *(Taeniatherum caput-medusae)* also are common in some areas. The region is considered high-elevation desert. Precipitation varies widely from mountain tops to valley bottoms with seasonal means ranging from 17 cm to 72 cm during winter and 10 cm to 150 cm during summer (PRISM Climate Group 2012). Temperatures are also highly variable across both annual and daily periods. Typical summer temperatures range between 45°C and −8°C, and winter temperatures are between 8°C and −16°C (PRISM Climate Group 2012).

Much of the study region is owned and managed by federal agencies including the BLM at lower elevations and the US Forest Service 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 land use in this region is livestock grazing on both private and federal lands, and other land uses are primarily recreational activities (e.g., hunting, fishing, hiking, camping, motorized and nonmotorized travel).

Modeling approach

We created inductive SDMs for sage-grouse and pygmy rabbits using maximum entropy (Maxent; Phillips et al. 2006; Phillips and Dudík 2008; Phillips et al. 2017a, 2017b). Maxent is a machine-learning SDM program that employs a set of occurrence locations, random background points, and predictor variables (geographical information system layers) to model the environmental niche or conditions typical of occupied habitat. It projects that model into geographic space, estimating the relative probability of species presence across the model region based on the environmental similarity to occupied sites. Models predict potential habitat distribution but not occupancy, which can depend on many factors such as site quality, land use and anthropogenic disturbance (direct and indirect), the amount and spatial arrangement of suitable habitat patches (i.e., fragmentation), proximity to occupied habitat, availability of seasonal habitats, and biotic interactions.

We developed four SDMs for sage-grouse: three seasonal models pertaining to spring (March 1–June 30); late brood-rearing (LBR; July 1–Sep 22; females, broods, and chicks); and winter (Dec 1–Feb 29) habitat use periods and a general distribution model for the entire annual cycle. Because pygmy rabbits are resident species, we created a single annual SDM.

Sage-grouse observations

We compiled > 228 000 sage-grouse observations in the study area stemming from very high frequency and Global Positioning System (GPS) telemetry studies, targeted sage-grouse surveys, and incidental observations (IDFG unpublished data). 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 < 400 m and dates could be attributed to a season (i.e., habitat use period). In addition, we reduced GPS-telemetry records to one randomly selected location per bird per day. We also removed observations that were within mapped fire perimeters (BLM 2018) collected before or within 5 yr after the fire discovery date, presuming that most fires were high severity or stand replacing and rendered the habitat unsuitable. This 5-yr time lag was designated 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 yr post fire. After screening, we retained > 53 000 observations of 875 marked birds and nearly 2 000 observations of unmarked birds. To reduce sampling bias, we pooled nearby observations into a 90-m pixel-centered presence location. For seasonal models, we selected observations in spring (males and females); LBR (females, broods, and chicks only); and winter (males and females). For the general distribution model we used all presence locations regardless of season and further reduced locally dense locations by randomly subsampling with a minimum distance of 180 m using SDMToolbox (Brown et al. 2017, 2018). The number of locations used to train and test the four sage-grouse models are shown in Table 1.

Pygmy rabbit observations

We compiled > 1 300 pygmy rabbit locations from field surveys for burrows (Roberts 2001), reference locations for collection of pygmy rabbit specimens or photographs, and incidental records collected by state and federal biologists. In addition, several studies of pygmy rabbit ecology have been conducted in this region, which contributed locations from live captures and radio telemetry (e.g.,

Table 1
Number of sage-grouse (SG) and pygmy rabbit (PR) locations used to model distribution in east-central Idaho. Maxent randomly sampled presence locations to train and test each model (split 70:30% for sage-grouse and 80:20% for pygmy rabbits, respectively) and used a background sample of random locations to represent the range of environmental conditions available in the study area.

Model	No. of locations	Maxent samples		
		Presence locations		Background
		Training	Testing	
SG general	15 988	11 192	4 796	47 900
SG spring	14 896	10 428	4 468	47 900
SG LBR	8 099	5 670	2 429	47 900
SG winter	4 380	3 066	1 314	47 900
PR annual	248	198	50	10 000

Sanchez and Rachlow 2008; 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 (e.g., pygmy rabbit pellets at burrow sites, photographs, visual confirmation, or field specimen collection). We filtered the trusted locations using a distance of 800 m to correspond to the coarsest-resolution environmental data (i.e., bioclimatic variables) used in the pygmy rabbit SDM, resulting in 248 locations for model training and testing (Table 1).

Environmental variables

To estimate distribution, we selected predictor variables related to land cover, topography, soil properties, climate, and phenology (Table 2 for variable descriptions, scales, and data sources). While the spatial resolution of all variables was 90 m, we characterized conditions at multiple spatial scales using focal statistics and various-sized neighborhoods that were based on sage-grouse movements and ecology. At fine scales (90-m, 200-m radius circular neighborhood), we characterized aspects of an occupied site or an immediate neighborhood surrounding a location to account for the spatial uncertainty inherent in the observation data. The mid-scale (1 000 m radius circular neighborhood) reflects average daily movements of GPS-marked sage-grouse (IDFG unpublished data). The broad scale (5 000-m circular neighborhood) aligns with analyses of landscape patterns and lek persistence (Knick et al. 2013), as well as guidelines to protect breeding habitat for nonmigratory populations of sage-grouse within 5 km of occupied leks (Connelly et al. 2000).

Land cover

We selected land cover variables that are known to influence the distribution of both sage-grouse and pygmy rabbits (see Table 2) from the National Land Cover Database land cover (USGS 2014), provisional shrubland components (USGS 2016a; USGS 2017a), and tree canopy cover datasets (USGS 2016b). We included four sagebrush metrics: mean sagebrush canopy cover and height at the fine scale and the proportion of the landscape with at least 10% canopy cover at mid and broad scales. This canopy cover threshold is related to the minimum requirements for sage-grouse winter habitat, although breeding requirements are generally higher (between 15% and 25%; Connelly et al. 2000). Pygmy rabbits have been documented in areas of sagebrush cover as low as 21% (Lee et al. 2010; Camp et al. 2013). We 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 by both species (Baruch-Mordo et al. 2013). Lastly, we quantified the amount of agriculture at fine, mid, and broad scales, expecting that sage-grouse would also generally avoid intensive agriculture, even though they may use agricultural lands adjacent to sagebrush habitats during the LBR season.

Topography

Topography and landform may influence distribution by altering growing conditions for vegetation and affecting weather at microsites (e.g., by diverting wind and snow). Although not always identified as important indicators of habitat quality, topography impacts biological processes and can serve as a proxy for some processes operating at finer scales than interpolated bioclimatic data (Guisan and Thuiller 2005; Lassueur et al. 2006). We calculated mean elevation and terrain roughness (i.e., standard deviation of elevation) at the fine scale. Topographic position refers to the normalized difference between elevation at a central pixel and the surrounding average elevation within a defined neighborhood (Weiss 2001), and we selected 500-m and 2 000-m focal radii to represent slope position and general landforms (see Table 2).

Soil properties

For the pygmy rabbit model, we estimated mean values of six soil characteristics (bulk density, calcium carbonate percentage, clay percentage, sand percentage, silt percentage, and pore size distribution; see Table 2) by averaging all depth bins within 1 m using POLARIS soils data (Chaney et al. 2016). Although the depth bins are of unequal size (i.e., 0–5 cm, 5–15 cm, 15–30 cm, etc.), we averaged them equally to effectively emphasize soil properties nearer to the surface because they have a strong influence on an animal's decision to continue digging. We also included depth to the restrictive layer, which was a single value (not averaged). Pygmy rabbits are obligate burrowers (Green and Flinders 1980) and 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. The heterogeneous distribution of soils characteristics 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). We did not include soil properties in the sage-grouse models because we do not know of studies that address how soil characteristics might directly influence distribution of sage-grouse; we assume that soil primarily affects sage-grouse habitat use through the vegetative community and, therefore, any relationships would be manifest in the vegetation data.

Climate and phenology

Climate can affect both vegetation and soil characteristics, especially in highly seasonal environments such as our study area. While sage-grouse can and will move to favorable microclimates, 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). We calculated 19 bioclimatic variables patterned after Hijmans et al. (2005) from monthly temperature and precipitation normals (i.e., long-term datasets describing average conditions from 1981 to 2010; PRISM Climate Group 2012) to include in the pygmy rabbit model (Table S1; available online at …). These variables have been used extensively in species distribution modeling (e.g., Elith et al. 2006; Anderson and Gonzalez 2011; Stanton et al. 2012), including pygmy rabbits (Smith et al. 2019), to capture the climatic envelope within which species persist.

Green vegetation (i.e., forbs) and associated insects are important resources to sage-grouse during the LBR season and provide quality forage for pygmy rabbits. To characterize late-summer (July 1–Sept 22) vegetation productivity or "greenness" across the study

Table 2
Environmental variables used to model general and seasonal distribution for sage-grouse and annual distribution for pygmy rabbits, as indicated by bullets. All variables were 90-m resolution. Scale refers to the area or neighborhood used in variable calculations (i.e., focal statistics).

Type	Environmental variable	Sage-grouse models				Pygmy rabbit model	Scale radius (meters)	Data source; notes
		General	Spring	LBR	Winter			
Land cover	Mean sagebrush cover (%)	•	•	•	•	•	200	Provisional remote sensing shrub/grass NLCD products (USGS 2016a; USGS 2017a); 2013 and 2014 source imagery
	Mean sagebrush height (cm)		•	•	•	•	200	
	Proportion of landscape with ≥ 10% sagebrush cover	•	•	•	•	•	1 000	
		•	•	•	•	•	5 000	
	Mean tree canopy cover (%)	•	•	•	•	•	200	NLCD 2011 USFS tree canopy (analytical version) (USGS 2016b)
	Proportion of landscape with > 3% forest canopy cover	•	•	•	•	•	1 000	
		•	•	•	•	•	5 000	
	Percentage of agriculture (%)	•	•	•	•	•	200	NLCD 2011 Land Cover (USGS 2014)
	Proportion of landscape in agriculture (%)	•	•	•	•	•	1 000	
		•	•	•	•	•	5 000	
Topography	Mean elevation	•	•	•	•	•	200	30-m Digital Elevation Model (USGS 2017b), Dilts (2015) [TPI]; TPI is the difference between elevation at a central point and the surrounding average elevation
	Terrain roughness; SD of elevation	•	•	•	•	•	200	
	Topographic Position Index (TPI), normalized	•	•	•	•	•	500	
		•	•	•	•	•	2 000	
Phenology	Mean NDVI during LBR season; avg. of monthly maximums			•		•	90	Normalized Difference Vegetation Index (NDVI) (USGS 2016c); an index to photosynthetic activity or vegetation greenness. Metrics were calculated annually, averaged from 2000 to 2016, and then resampled from 250 m to 90 m using the nearest neighbor.
	Variability in NDVI during LBR season; SD of monthly maximums			•		•	90	
Climate	19 bioclimatic variables (Hijmans et al. 2005)					•	90	PRISM 30-yr normals of precipitation and temperature (PRISM Climate Group 2012); resampled from 800 m to 90 m using nearest neighbor.
Soil Properties	Mean soil available water capacity in the first meter (m^3/m^3)					•	90	POLARIS soil data (Chaney et al. 2016).
	Mean soil bulk density in the first meter (g/cm^3)					•	90	
	Mean percentage of calcium carbonate in soil in the first meter					•	90	
	Pore size distribution index (Brooks and Corey 1964)					•	90	
	Depth to restrictive layer (cm)					•	90	
	Mean percentage of sand in soil in the first meter					•	90	
	Mean percentage of silt in soil in the first meter					•	90	

area, we used the normalized difference vegetation index (NDVI; USGS 2016c), which is a widely used remote sensing measure of green biomass and a good indicator of drought. We used cloud-free eMODIS 7-d composite NDVI images (USGS 2016c) to calculate mean monthly maximum NDVI for July, August, and September and then quantified the mean intraseasonal average and standard deviation from 2000 to 2016 (see Table 2). We assumed that sage-grouse hens and broods would use areas with relatively high and persistent vegetation productivity during the LBR season, as would pygmy rabbits. We did not use these phenology variables for other sage-grouse SDMs because they were season specific.

We manipulated all spatial data in ArcGIS 10.3.1 (ESRI 2016), ensuring a common geographic coordinate system, spatial resolution (90 m), and extent and then exported variables as ASCII files for input into program R 3.5.2 (R Core Team 2018) and Maxent 3.4.0 (Phillips et al. 2017a). We constructed a pairwise correlation matrix for all variables to note which were highly correlated, checking that each variable was a plausible predictor (i.e., frequency distribution at species locations was not constant across environmental gradients).

Model development, validation, and categorization

To contrast with presence locations and represent available environmental conditions, we generated species-specific background samples that consisted of random points drawn from the study area (see Table 1). We extracted the values of all environmental variables to both presence and background points and ran Maxent in samples-with-data format.

We fine-tuned 2 Maxent parameters—the regularization multiplier and feature types—using the R package *enmSdm* v0.3.4.6 (Smith 2019). The regularization multiplier imposes a penalty for

designing overly complex or overfit models. By increasing the multiplier, it smooths out the distribution 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 2013). Feature types are mathematical transformations of the variables used in a model (i.e., linear, quadratic, product, threshold, and hinge) that allow different shapes of variable response curves (Elith et al. 2011; Merow et al. 2013). Instead of using program defaults we tested a range of multipliers (from 0.5 to 5 in 0.5 increments, and 6 to 20 in 1.0 increments) and different combinations of feature types to identify the best performing combination based on sample size−corrected Akaike Information Criteria (AICc) (Warren and Seifert 2011; Wright et al. 2015). We applied these optimized parameters to Maxent, accepting other defaults and the option to add the presence sample to the background sample, and constructed SDMs inclusive of all variables considered ($n = 13$–16 for sage-grouse and $n = 42$ for pygmy rabbits; see Table 2).

We tested each model's predictive performance using 10-fold subsampling validation, whereby Maxent modeled suitability 10 ×, each time drawing a random subsample of locations to train the model and tested the prediction with the held-out sample (see Table 1). We assessed model fit to the held-out sample using the area under the receiver operating characteristics curve (AUC), which is a threshold-independent measure of a model's ability to discriminate presences from background points (Elith et al. 2010; Merow et al. 2013). We used jackknifing to measure the importance of each variable to the resulting prediction and ranked variables based on their permutation importance (PI; normalized to a percentage). PI is the measured drop in AUC when variable values, in turn, are randomly permuted, or changed, at training and background points; a larger PI means that a variable has a bigger influence on the overall Maxent prediction compared with other variables.

Next, we simplified models by removing variables that contributed little to the overall prediction (i.e., < 2% PI) or were highly correlated (Pearson's correlation > |0.8|) with other variables (we removed the variable with the smaller PI value in pairwise comparisons). With a reduced set of variables, we then constructed a "reduced" model, repeating the process of parameter optimization, model training and validation, variable ranking, and variable reduction until there were no highly correlated variables and all variables achieved at least 2% PI. The final (reduced) models represented the average of 10 model runs in cloglog format, which places the model values (i.e., species presence) on a probability scale between 0 and 1 (Phillips et al. 2017a, 2017b).

Spatial distribution model similarity and spatial overlap

We assessed model similarity and the spatial overlap of all SDMs. First, we used the raw prediction surfaces (i.e., continuous probability values) to calculate Pearson's correlation, Schoener's D index (Schoener 1968), and Warren's I statistic (Warren et al. 2010) using the R package ENMTools v1.0.1 (Warren and Dinnage 2020). These metrics all quantify similarity between SDMs 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 1 representing higher overlap. Unlike Schoener's D, Warren's I was developed specifically for presence-only SDMs (Warren 2008). Next, we categorized predictions in binary suitable/unsuitable maps to quantify the geometric overlap of potential habitat. To define potentially suitable habitat, we selected a threshold value that maximized the sum of testing sensitivity plus specificity. In other words, it maximized the number of cases where true presences and background points were correctly predicted among the held-out test data. This threshold is often used as a binomial classifier for presence-only SDMs because classification accuracy is more consistent when the ratio of presence locations to background points changes (Liu et al. 2005). For a comparison, we applied a second, higher threshold, the average predicted value at presence points, to better understand how geometric overlap depends on threshold choice. This higher threshold could be used to differentiate suitable from highly suitable areas, which might be desirable for targeting habitat improvements or protection easements where a species is most likely to occur.

Results

Sage-grouse SDMs

Potential sage-grouse habitat in our study area was relatively widespread and predicted throughout most mountain valleys and the eastern Snake River Plain but more fragmented toward the northern and western portion of the study area (Fig. 1a–d). Predicted habitat generally occurred at midelevations (between 1 500 and 2 000 m) where topography was relatively flat or gently sloped, tree canopy cover (at midscale) and agriculture (broad-scale for all seasons plus the fine-scale in winter) were lacking, and sagebrush was plentiful (Table 3). The proportion of the landscape with ≥ 10% sagebrush cover at the midscale was an influential variable in all models except the winter model, which was influenced more by broad-scale sagebrush cover (see Table 3). Although sagebrush height was not used in the general model, it influenced predicted distribution in all seasons. Distribution was generally correlated with taller sagebrush shrubs during spring and LBR seasons than in winter (Fig. S1; available online at …). LBR distribution was influenced by both the mean and variation of NDVI during the late brood-rearing period as expected, and predicted habitat occurred across a wider range and at slightly higher elevations relative to other seasons (see Fig. S1). Sage-grouse distribution models yielded highly accurate predictions, with AUC = 0.797 for the general model. Each seasonal model yielded higher AUC values (spring = 0.823, LBR = 0.854, and winter = 0.911), which was expected given that they were tailored to shorter time periods.

Among the sage-grouse seasonal models, predicted distribution was the most widespread during spring and most restricted during winter (see Fig. 1). Spring and female LBR model predictions were positively correlated and relatively similar ($r = 0.762$, $D = 0.748$, $I = 0.943$), as were spring and winter ($r = 0.789$, $D = 0.704$, $I = 0.929$), but LBR and winter models differed the most ($r = 0.375$, $D = 0.512$, $I = 0.803$; Table 4). Spatial overlap varied among seasons as well (Tables S2 and S3, Fig. 2). For example, spring and LBR shared 1 328 km^2 of the area predicted to be highly suitable habitat, spring and winter overlap was slightly less at 1 026 km^2, but winter and LBR overlap was only 72 km^2 (see Fig. 2b). A similar pattern is apparent among seasons for predicted suitable habitat (se Fig. 2a). Areas where spring and winter model predictions overlapped tended to occur at lower elevations than areas where spring and LBR overlapped. Although the eastern Snake River Plain in the southeastern portion of the study area supported a relatively large expanse of highly suitable habitat during both spring and LBR seasons, highly suitable winter habitat was lacking (see Fig. 1). There was also no suitable winter habitat predicted east of the Beaverhead Mountains along the northeastern margin of the study area. Compared with seasonal models, the general distribution model was most similar to the spring model ($r = 0.960$, $D = 0.898$, $I = 0.989$; see Table 4), which may be explained, in part, by the high number of spring locations relative to other seasons (see Table 1), but also likely a function of the variety of habitats used during spring, which includes lekking, nesting, and early brood-rearing habitat use periods.

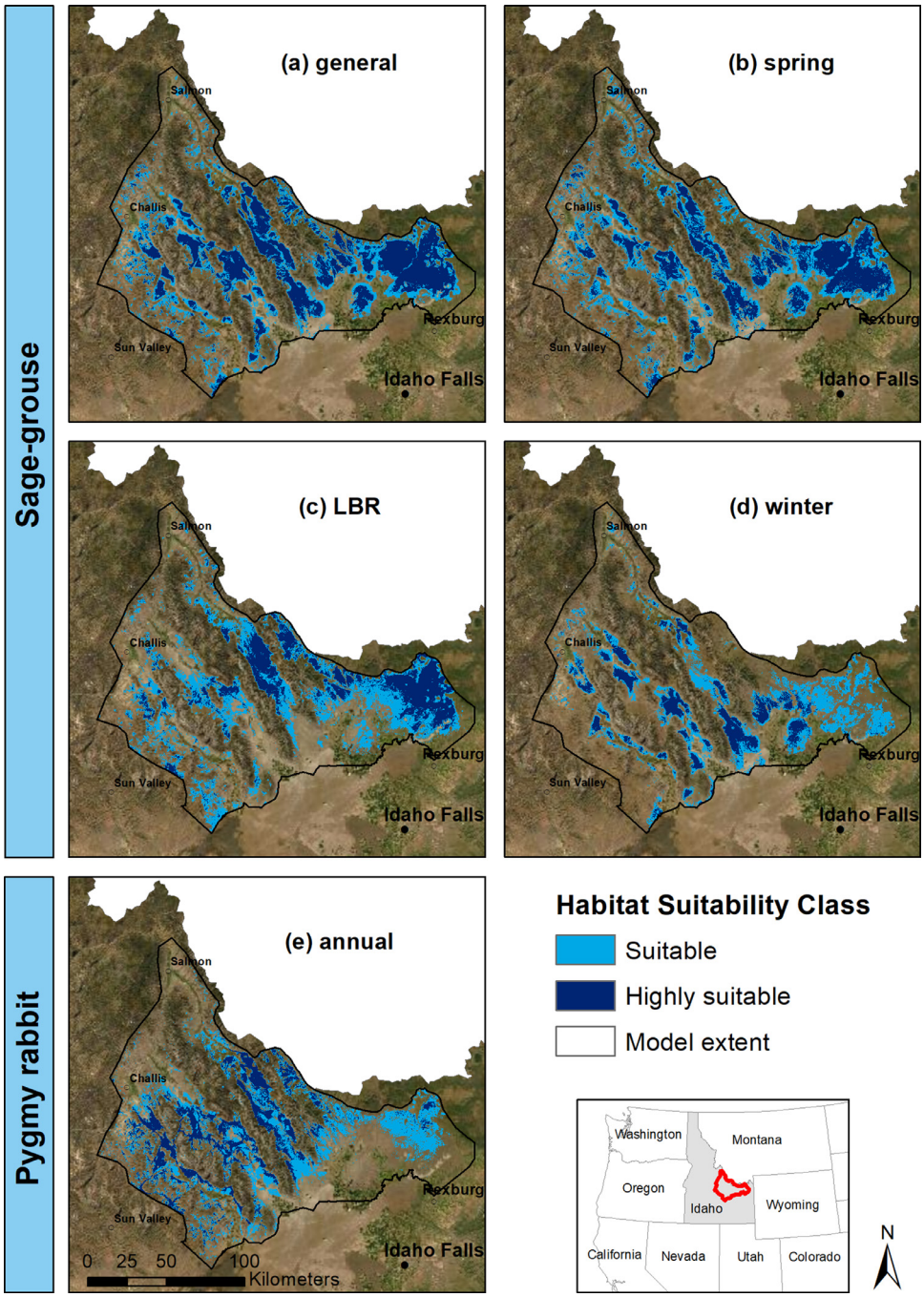


Figure 1. Predicted distribution models for sage-grouse and pygmy rabbits in east central Idaho. Models include (**a**) general, (**b**) spring (March 1–June 30), (**c**) late brood-rearing (LBR—females only; July 1–September 22), and (**d**) winter (December 1–February 29) distribution for sage-grouse, and an (**e**) annual model for pygmy rabbits because the species does not shift habitat use among seasons. Thresholds for suitable and highly suitable areas were values that maximized the sum of test sensitivity and specificity and the average predicted values at presence points, respectively.

Pygmy rabbit SDM

Predicted habitat for pygmy rabbits was fairly widespread and occurred in most mountain valleys and the eastern Snake River Plain but somewhat fragmented and less area than predicted sage-grouse habitat, especially considering highly suitable habitat (see Fig. 1e). Some of the most suitable areas occurred along the lateral edges of mountain valleys and at higher elevations, as well as in isolated sagebrush corridors between steeper mountainous terrain (i.e., canyons or ravines). These landforms are identified by moderately negative values for TPI at the 2 000-m resolution (see Fig. S1) that correspond to lower slopes, above valley floors (see Fig. 1e).

Distribution was characterized by 10 variables related to topography, vegetation, soil, climate, and phenology (see Table 3). The most influential variable was terrain roughness, indicating that pygmy rabbits occurred in relatively flat areas. Mean sagebrush cover at the fine scale and the proportion of landscape with ≥ 10% sagebrush at the broad scale were retained in the model after variable reduction. Like sage-grouse, predicted habitat for pygmy rabbits lacked trees, but canopy cover at the fine scale was more informative than either mid or broad scales. Two soil variables that

Table 3
Environmental variables used in the final sage-grouse and pygmy rabbit models, along with the relative variable importance (percent contribution/permutation importance), model fit (AUC), optimized model parameters (regularization multiplier and feature types), and thresholds applied to define potentially suitable and highly suitable habitat. A dash (—) indicates a variable that was not considered in model development.

Environmental variables	Sage-grouse models				Pygmy rabbit model
	General	Spring	LBR	Winter	
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 (%)					22.0/6.6
Percentage of agriculture (%)				12.5/8.0	
Proportion of landscape in sagebrush with ≥ 10% cover (1 000-m radius)	9.2/6.2	6.6/5.7	31.9/5.6		
Proportion of landscape in sagebrush with at least 10% cover (5 000-m radius)				6.1/6.9	0.7/2.6
Proportion of landscape with > 3% tree canopy cover (1 000-m radius)	51.0/43.9	61.0/45.6	14.7/32.6	62.3/39.7	
Proportion of landscape in agriculture (5 000-m radius)	19.6/14.1	6.6/10.2	4.3/9.7	4.0/12.0	
Mean elevation (m)	3.9/3.6	0.6/2.9	2.7/3.0	1.3/6.9	
Terrain roughness	12.9/23.2	5.3/12.4	21.0/26.5	6.7/12.5	28.9/34.9
Topographic Position Index (500-m radius)		1.5/4.0		1.1/3.7	
Topographic Position Index (2 000-m radius)	3.5/9.1	2.9/9.5	1.8/4.4	2.8/8.0	5.2/7.5
Mean Normalized difference vegetation index (NDVI) during LBR	—	—	1.5/4.3	—	12.8/10.5
Normalized difference vegetation index (NDVI) variability during LBR	—	—	5.7/8.4	—	
Pore size distribution index	—	—	—	—	2.2/4.2
Percentage of silt in soil	—	—	—	—	4.6/9
Temp. of the warmest quarter	—	—	—	—	19.1/12.4
Temp. of the coldest quarter	—	—	—	—	0.4/2.6
Area under the receiver operating characteristic curve (AUC)	0.797	0.823	0.854	0.911	0.854
Regularization multiplier	0.5	0.5	0.5	0.5	0.5
Feature types: l = linear, q = quadratic, p = product, h = hinge	l, q, p, h	l, q, p, h	l, q, p, h	l, q, p, h	l, q
Thresholds: Maximum Test Sensitivity Plus Specificity / Average predicted values at presence locations	0.42/0.65	0.38/0.66	0.32/0.65	0.28/0.67	0.35/0.65

Table 4
Measures of similarity between distribution models for sage-grouse (general and seasonal) and pygmy rabbits in east-central Idaho. Pearson's correlation (r; shown above the diagonal) is ($P < 0.0001$ for all r based on 1 000 sample points). Similarity indices, Schoener's D (Schoener 1968) m, and the I statistic (Warren et al. 2008) are shown below the diagonal.

Models	General	Spring	LBR	Winter	Pygmy rabbit
General		0.960	0.812	0.753	0.666
Spring	D = 0.898 I = 0.989		0.762	0.789	0.567
LBR	D = 0.781 I = 0.957	D = 0.748 I = 0.943		0.375	0.606
Winter	D = 0.668 I = 0.908	D = 0.704 I = 0.929	D = 0.512 I = 0.803		0.429
Pygmy rabbit	D = 0.702 I = 0.912	D = 0.656 I = 0.882	D = 0.665 I = 0.894	D = 0.530 I = 0.795	

LBR indicates late brood-rearing.

reflect soil texture and permeability, silt percentage and pore size distribution, influenced predicted distribution (highest suitability occurred at intermediate values, ~35% and ~0.37, respectively). Likewise, two bioclimatic variables representing thermal extremes (the mean temperature of the warmest quarter and the mean temperature of the coldest quarter of the year) were influential, and distribution correlated with intermediate values (i.e., ~14°C for warmest quarter and ~−7.5°C for coldest quarter temperatures, see Fig. S1). The pygmy rabbit model had an AUC of 0.854, indicating high discriminatory power.

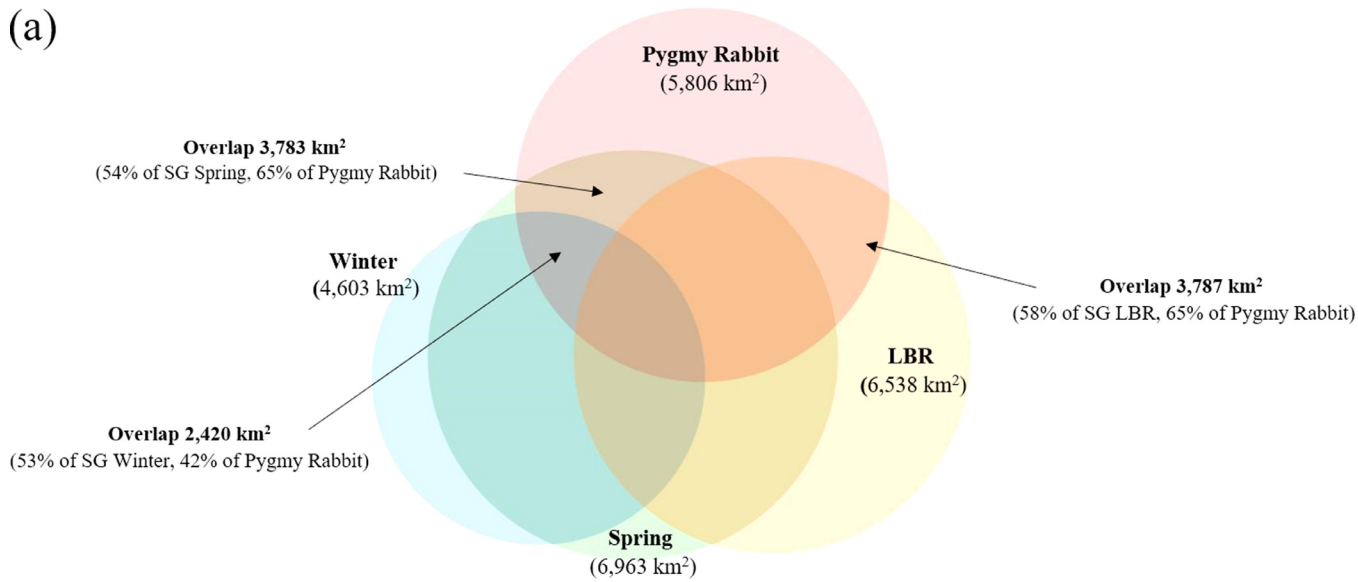
Species overlap

As expected, there was considerable overlap between predicted habitat for sage-grouse and pygmy rabbits in our study region. Overall, general sage-grouse and pygmy rabbit distributions were positively and significantly related and highly similar ($r = 0.67$, D = 0.70, I = 0.91; see Table 4). Potential sage-grouse distribution encompassed 73% of all suitable habitat predicted for pygmy rabbits, but this proportion dropped to 49% when considering highly suitable habitat (Table S3; available online at …). Most overlap of highly suitable habitat occurred at higher elevations in the major valleys of the study area and along the margins of the valley bottoms (Fig. 3). This pattern was a consequence of the distribution of pygmy rabbit habitat, which included smaller areas at higher elevations than sage-grouse. Highly suitable sage-grouse habitat was more widely distributed, and the species tended to occur at lower elevations than pygmy rabbits. Also, the southeastern portion of the study area on the eastern Snake River Plain contained a large area of highly suitable habitat for sage-grouse but not for pygmy rabbits, demonstrating substantial spatial differences at the regional extent (see Fig. 3).

Contrary to our expectation that species overlap would be highest during spring, overlap was nearly identical during the spring and LBR seasons, regardless of threshold used. For example, the predicted area of overlap was 3 783 km^2 (65%) of suitable habitat for spring and 3 878 km^2 (65%) for suitable LBR habitat (Table S2, available online at …; Fig. 2), which was more than 1.5 × as high as during winter (2 420 km^2; 42%). Similarly, the proportion of highly suitable spring and female LBR habitat comprised 675 km^2 (30%) and 685 km^2 (31%) of highly suitable pygmy rabbit habitat, respectively, in contrast to only 404 km^2 (18%) during winter (Table S3, available online at …; Fig. 2). In addition, overlap between species during winter was the most spatially dispersed of all seasons and occurred in relatively small patches.

Discussion

Sagebrush conservation in the western United States has centered on protecting areas used by sage-grouse, an iconic umbrella species. Although overlap between sage-grouse and another sagebrush-obligate, the pygmy rabbit, is high at the extent of the species range (Smith et al. 2019), we documented lower and variable co-occurrence at a regional extent and seasonal time periods. Considering the general distribution for sage-grouse, 73% of predicted suitable habitat for pygmy rabbits in our study area was encompassed by suitable habitat for sage-grouse, and overlap decreased to 42–65% during individual seasons. However, these proportions dropped significantly if we considered overlap of highly



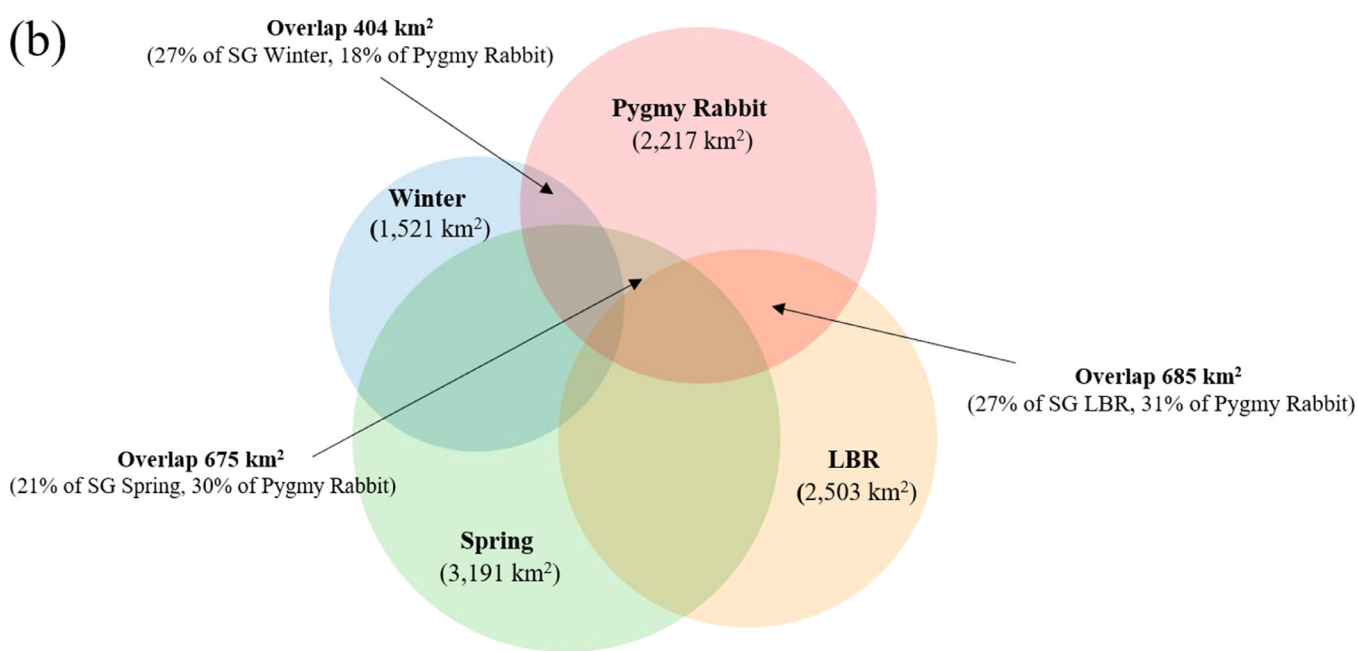


Figure 2. Proportion and area of predicted overlap of (**a**) suitable habitat and (**b**) highly suitable habitat for seasonal (spring, late brood-rearing, and winter) sage-grouse and annual pygmy rabbit models in east-central Idaho.

suitable habitat; only 49% of highly suitable predicted habitat for pygmy rabbits fell within highly suitable sage-grouse habitat, and seasonal overlap decreased to 18–31%. To be effective, applications of surrogate species strategies (e.g., umbrella species) need to be designed at scales consistent with conservation actions. Our work suggests that even though pygmy rabbits are tightly coupled with the sagebrush ecosystem, their conservation and management at regional scales will require additional consideration of habitats and locations outside of areas known to be primary sage-grouse habitat. This work provides a cautionary tale for conservation strategies that employ surrogate species or other heuristic approaches to conservation planning without consideration of how overlap might vary across spatiotemporal scales, especially in seasonal environments.

Our study area can be visualized as a semidichotomous landscape made up of either basins and rolling plains covered primarily by sagebrush steppe, agriculture and other anthropogenic land use, or forested mountains with rugged terrain. Sage-grouse, predictably, occurred in the basins and plains areas with relatively high sagebrush cover, away from agriculture and forests. The seasonal distributions of highly suitable habitat for sage-grouse shifted as expected in both spatial and environmental terms. The relatively low level of predicted overlap between the LBR model for females and the winter model reflects the migratory nature of sage-grouse populations in this landscape. Sage-grouse in our study area have previously been documented moving up to 80 km during summer following phenological shifts in green vegetation (Klebenow 1969; Connelly et al. 1988). Use of a greater range of

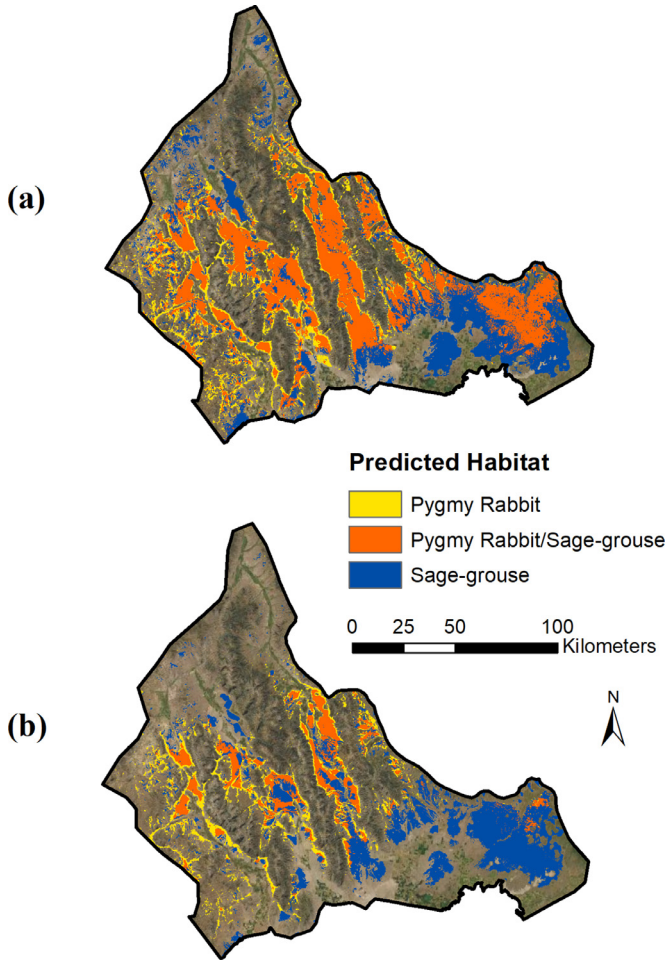


Figure 3. The spatial overlap of predicted (**a**) suitable habitat and (**b**) highly suitable habitat for sage-grouse (general distribution model) and pygmy rabbit in east-central Idaho. Maps were combined after thresholds were applied to the spatial distribution models' probability values; suitable habitat was defined by the threshold that maximized test sensitivity and specificity, whereas highly suitable habitat was defined by the average predicted value at presence locations.

elevations by females during the LBR season probably reflects gradual movements to higher elevations in response to vegetation phenology. Further, relatively high seasonal overlap between winter and spring and spring and female LBR habitat may reflect gradual transitions among seasonal habitat that depend on annual conditions. As we hypothesized (H1), these habitat associations are consistent with a general understanding of sage-grouse habitat selection at multiple scales (e.g., Connelly et al. 2000; Aldridge et al. 2008; Baruch-Mordo et al. 2013; Knick et al. 2013).

The distribution of pygmy rabbits in the study region was influenced by topography, vegetation, climate, soil characteristics, and phenology, and the habitat variables in the final model generally matched our expectations (H2). In contrast to sage-grouse, the distribution of pygmy rabbits was shaped by relatively finer-scale variables, which likely reflects more restricted mobility, space use, and possibly even greater habitat specialization. For example, sagebrush cover at the fine scale (i.e., 200-m radius, 9.7% permutation importance) was more influential than the broad-scale variable (≥ 10% sagebrush cover at a 5 000-m radius; 2.7% permutation importance). In contrast, all sage-grouse predictions were influenced more by sagebrush cover at either the mid or broad scales than at the fine scale (see Table 3). Although previous research conducted at finer scales reported selection by pygmy rabbits for areas farther from sagebrush edges (Pierce et al. 2011), other habitat factors might constrain use of areas within more continuous sagebrush landscapes in our study area. Finally, although the distribution of pygmy rabbits might be strongly affected by soil characteristics, soil data available over relatively large extents are unlikely to map fine-scale heterogeneity in the distribution of soils properties that constrain occupancy by this burrowing species.

We expected species overlap to decline at finer spatial and temporal scales (H3), and a comparison with range-wide analyses of co-occurrence (Smith et al. 2019) supports this expectation. Predicted overlap between highly suitable habitat for sage-grouse (the general distribution model) and pygmy rabbits in our study area (49%) was lower than similar estimates across the range of pygmy rabbits (91%; Smith et al. 2019) and was even lower and more variable among seasons (18–31%). Furthermore, the spatial pattern of overlap was not consistent across the study area. These results underscore the importance of evaluating species overlap across temporal scales to design habitat conservation strategies that benefit multiple species. When target species are also migratory, temporal considerations of species overlap become even more important in designing management strategies (e.g., mule deer; Copeland et al. 2014).

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 co-occurrence of sage-grouse and pygmy rabbits; however, we did not attempt to quantify this. Availability of highly palatable sagebrush (i.e., sagebrush with less monoterpenes and indigestible fibers) is an important resource for both species (e.g., Weiss and Verts 1984; Frye et al. 2013; Ulappa et al. 2014). It is possible that sage-grouse and pygmy rabbits, along with other small herbivores, might compete for sagebrush cover in favored microhabitats, however, we are not aware of studies that have examined these possibilities, and to our knowledge, there is no evidence indicating that this resource is limiting.

Our species distribution and overlap estimates are based on modeling processes with inherent biases that stem from both ecological and statistical assumptions and data limitations. We used generally accepted best modeling practices to reduce sampling bias by spatial subsampling occurrence records and by tuning model regularization multipliers (Merow et al. 2014; Searcy and Shaffer 2016). Although Maxent is robust to collinearity, we removed correlated variables and reduced the number of variables used in our models to limit complexity and help with model interpretation (Merow et al. 2014) with only marginal decreases in AUC (model fit). Commission errors may be more common than usual in our pygmy rabbit model 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 2009). Using thresholds to create habitat suitability categories is also 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 (see Fig. 3). Nevertheless, we selected reasonable thresholds that could apply to management scenarios. None of the SDMs considered anthropogenic impacts (direct or indirect) and thus are likely to overestimate suitable distribution. Finally, there was a large disparity in the numbers of locations used to build models for sage-grouse and pygmy rabbits, which reflects the degree to which the species have been studied. We did not explore how this disparity might influence our models. However, given that the training locations we used for both the pygmy rabbit and sage-grouse models were well dispersed across the known range of the respective species in the region, we assume to have captured much of the range of habitat conditions occupied and suspect the effects of such disparity in sample size are limited. A lack of representation is more concerning than sample size, although these factors can be related.

An obligate relationship with sagebrush, use of large and heterogenous landscapes, and sensitivity to anthropogenic disturbance make the sage-grouse an obvious choice for a system-wide umbrella species, but sage-grouse may be a better surrogate for other birds than for mammals (Carlisle et al. 2018; Timmer et al. 2019). Even among sagebrush obligate birds, however, sage-grouse might not be appropriate umbrellas at finer scales or when considering abundances of target species (Carlisle and Chalfoun 2020). 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; Lentini and Wintle 2015). For example, a large forest grouse, the Capercaillie *(Tetrao urogallus),* serves as an umbrella species in the Swiss Prealps, and study plots with these grouse had higher species richness and abundance of mountain birds of conservation concern than in those without Capercaillie (Suter et al. 2002). However, the ostensible use of sage-grouse as an umbrella species for sagebrush-associated wildlife may prove inadequate for species with more particular habitat needs (Timmer et al. 2019) or with lower dispersal abilities like many small mammals. For example, protection of sage-grouse habitat may facilitate persistence of pygmy rabbits in certain sagebrush patches (i.e., areas deemed priority habitat for sage-grouse); however, if these patches are not well connected, pygmy rabbits might experience population declines with little opportunity for population rescue through natural immigration given their relatively limited dispersal abilities.

Although pygmy rabbits and sage-grouse share many habitat requirements, fundamental differences in their ecology and life history underscore the need for management plans or conservation strategies that also consider individual species or groups of species. Pygmy rabbits rely on soils that are suitable for burrowing; thus, they use a narrower range of habitats and occupy smaller areas than sage-grouse. Consequently, pygmy rabbits might serve as a surrogate for other sagebrush species that also require friable soils conducive to holding burrow structure (e.g., sagebrush vole, *Lemmiscus curtatus*). Through burrowing activities, pygmy rabbits also serve as ecosystem engineers that influence many other species and processes, including sagebrush regeneration (Parsons et al. 2016). Because conservation efforts may be most effective when they target key ecosystem engineers (Odling-Smee et al. 2003; Boogert et al. 2006), we suggest that land managers incorporate additional protection for pygmy rabbits, especially where pygmy rabbit habitat falls outside of areas designated as primary for sage-grouse.

Effective 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). Because limited availability of resources often leads to simplified strategies for conservation and the use of umbrella species is likely to continue, defining areas of high and low spatial overlap between species of conservation concern will remain a critical part of managing areas for multiple uses and for wildlife conservation (Dobson et al. 1997; Andelman and Fagan 2000). Identifying where and when species are sympatric and when they are not will increase the effectiveness of conservation strategies involving surrogate species.

Implications

Our approach to evaluating seasonal co-occurrence of sage-grouse and pygmy rabbits has implications for conservation of these species in east-central Idaho and across their ranges. Our results suggest that inclusion of areas outside of sage-grouse habitats will be needed to encompass highly suitable habitat for pygmy rabbit populations. In our study area, narrow corridors of suitable habitat for pygmy rabbits were identified along lower slopes, above valley floors, and these areas were often not encompassed within the habitats predicted for sage-grouse. Habitat considered highly suitable for pygmy rabbits, but not for sage-grouse, generally occurs on the fringes of highly suitable habitat for both species. Therefore, to provide more protection to pygmy rabbit habitat, managers might consider conservation measures within a slightly larger area (i.e., 1−2 km buffer) of mapped highly suitable habitat for both species.

This work also demonstrates how species overlap can change across space and time, even for species that are highly specialized on similar resources. Evaluations of the sage-grouse umbrella should take into consideration the migratory nature of the target species. Future research could evaluate temporal dimensions when considering spatial overlap, which might be especially important for sagebrush obligate songbirds. More generally, this work provides a cautionary tale for the use of umbrella species at regional or local scales without studies to evaluate co-occurrence between the umbrella and other species of conservation concern.

Declaration of Competing Interest

None.

Acknowledgments

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.06.007.

References

Aldridge, C.L., Nielsen, S.E., Beyer, H.L., Boyce, M.S., Connelly, J.W., Knick, S.T., Schroederm, M.A., 2008. Range-wide patterns of greater sage-grouse persistence. Diversity & Distributions 14, 983–994.

Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences 97, 5954–5959.

Anderson, R.P., Gonzalez, I., 2011. Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecological Modelling 222, 2796–2811.

Araújo, M.B., Rozenfeld, A., Rahbek, C., Marquet, P.A., 2011. Using species co-occurrence networks to assess the impacts of climate change. Ecography 34, 897–908.

Back, G.N., Barrington, M.R., McAdoo, J.K., 1987. Sage grouse use of snow burrows in northeastern Nevada. Wilson Bulletin 99, 488–490.

Barlow, N.L., Kirol, C.P., Doherty, K.E., Fedy, B.C., 2019. Evaluation of the umbrella species concept at fine spatial scales. Journal of Wildlife Management 84, 237–248.

Baruch-Mordo, S., Evans, J.S., Severson, J.P., Naugle, D.E., Maestas, J.D., Kiesecker, J.M., Falkowski, M.J., Hagen, C.A., Reese, K.P., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biological Conservation 167, 233–241.

Boogert, N.J., Paterson, D.M., Laland, K.N., 2006. The implications of niche construction and ecosystem engineering for conservation biology. BioScience 56, 570–578.

Borell, A.E., Ellis, R, 1934. Mammals of the Ruby Mountains region of north-eastern Nevada. Journal of Mammalogy 15, 12–44.

Braun, C.E., Connelly, J.W., Schroeder, M.A., 2005. Seasonal habitat requirements for sage-grouse: spring, summer, fall, and winter. In: Shaw, N.L., Pellant, M., Monsen, S.B. (Eds.), Sage-grouse Habitat Restoration Symposium, Proceedings of the Rocky Mountain Research Station-P-38; 4-7 June 2001, Fort Collins, CO, USA, pp. 38–42.

Bradshaw, W.E., Holzapfel, C.M., 2007. Evolution of animal photoperiodism. Annual Review of Ecology 38, 1–25 *Evolution & Systematics*.

Brooks, R., Corey, T, 1964. Hydraulic properties of porous media. Hydrology Papers, No.. Colorado State University, Fort Collins, CO, USA, p. 37.
Brown, J.L., Bennett, J.R., French, C.M., 2018. SDMtoolbox v2.3 (for ArcMap 10.1–10.3) Available at: http://sdmtoolbox.org.
Brown, J.L., Bennett, J.R., French, C.M., 2017. SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. PeerJ 5, e4095.
Butler, S.J., Freckleton, R.P., Renwick, A.R., Norris, K, 2012. An objective, niche-based approach to indicator species selection. Methods in Ecology & Evolution 3, 317–326.
Bureau of Land Management (BLM), 2015. Record of decision and approved resource management plan amendments for the Great Basin region, including the greater sage-grouse sub-regions of Idaho and Southwestern Montana. US Department of the Interior, Bureau of Land Management, Washington, DC, USA.
Bureau of Land Management (BLM), 2018. Fire perimeters historic. Polygon digital dataset. Bureau of Land Management, Idaho State Office, Boise, ID, USA.
Camp, M.J., Rachlow, J.L., Woods, B.A., Johnson, T.R., Shipley, L.A., 2013. Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat. Ecosphere 4, 1–14.
Carlisle, J.D., Chalfoun, A.D., 2020. The abundance of Greater Sage-Grouse as a proxy for the abundance of sagebrush-associated songbirds in Wyoming, USA. Avian Conservation and Ecology 15, 16.
Carlisle, J.D., Keinath, D.A., Albeke, S.E., Chalfoun, A.D., 2018. Identifying holes in the greater sage-grouse conservation umbrella. Journal of Wildlife Management 82, 948–957.
Caro, T.M., 2003. Umbrella species: critique and lessons from East Africa. Animal Conservation 6, 171–181.
Caro, T.M., O'Doherty, G, 1999. On the use of surrogate species in conservation biology. Conservation Biology 13, 805–814.
Chaney, N.W., Wood, E.F., McBratney, A.B., Hempel, J.W., Nauman, T.W., Brungard, C.W., Odgers, N.P., 2016. POLARIS: A 30-meter probabilistic soil series map of the contiguous United States. Geoderma 274, 54–67.
Coates, P.S., Delehanty, D.J., 2010. Nest predation of greater sage-grouse in relation to microhabitat factors and predators. Journal of Wildlife Management 74, 240–248.
Connelly, J.W., Browers, H.W., Gates, R.J., 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52, 116–122.
Connelly, J.W., Wakkinen, W.L., Apa, A.D., Reese, K.P., 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55, 521–524.
Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28, 967–985.
Connelly, J.W., Rinkes, E.T., Braun, C.E, 2016. Characteristics of greater sage-grouse habitats: a landscape species at micro- and macroscales. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian BiologyUniversity of California Press, pp. 69–83 No. 38. Berkeley, CA, USA.
Copeland, H.E., Sawyer, H., Monteith, K.L., Naugle, D.E., Pocewicz, A., Graf, N., Kauffman, M.J., 2014. Conserving migratory mule deer through the umbrella of sage–grouse. Ecosphere 5, 1–16.
Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144, 2573–2584.
DeLong, A.K., Crawford, J.A., DeLong Jr., D.C., 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59, 88–92.
Dalke, P.D., Pyrah, D.B., Stanton, D.C., Crawford, J.E., Schlatterer, E.F., 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27, 811–841.
Dilts, T., 2015. Topography tools for ArcGIS 10.1 and earlier. University of Nevada Reno. Available at https://www.arcgis.com/home/item.html?id=b13b3b40fa3c43d4a23a1a09c5fe96b9.
Affairs, Division of Public, 2015. Historic conservation campaign protects greater sage-grouse. US Fish and Wildlife External Affairs, Washington, DC, USA.
Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. Science 275, 550–553.
Donnelly, J.P., Naugle, D.E., Hagen, C.A., Maestas, J.D., 2016. Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions. Ecosphere 7, e01208.
Drut, M.S., Crawford, J.A., Gregg, M.A., 1994. Brood habitat use by sage grouse in Oregon. The Great Basin Naturalist 54, 170–176.
Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.
Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Diversity & Distributions 17, 43–57.
ESRI, 2016. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA, USA Release 10.3.1..
Estes-Zumpf, W.A., Rachlow, J.L., 2009. Natal dispersal by the pygmy rabbit *(Brachylagus idahoensis)*. Journal of Mammalogy 90, 363–372.
Estes-Zumpf, W.A., Rachlow, J.L., Waits, L.P., Warheit, K.I., 2010. Dispersal, gene flow, and population genetic structure in the pygmy rabbit *(Brachylagus idahoensis)*. Journal of Mammalogy 91, 208–219.
Favreau, J.M., Drew, C.A., Hess, G.R., Rubino, M.J., Koch, F.H., Eschelbach, K.A., 2006. Recommendations for assessing the effectiveness of surrogate species approaches. Biodiversity & Conservation 15, 3949–3969.
Register, Federal, 2004. Endangered and threatened wildlife and plants; 90-day finding for petitions to list the greater sage-grouse as threatened or endangered. Federal Register 69, 21484–21494.
Register, Federal, 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the pygmy rabbit as endangered or threatened. Federal Register 75, 60515–60561.
Frye, G.G., Connelly, J.W., Musil, D.D., Forbey, J.S., 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94, 308–314.
Green, J.S., Flinders, J.T., 1980. Habitat and dietary relationships of the pygmy rabbit. Journal of Range Management 33, 136–142.
Grinnell, J., Dixon, J.S., Linsdale, J.M., 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. University of California Press, Berkeley, CA, USA 594 pages.
Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993–1009.
Hanser, S.E., Knick, S.T., 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology No. 38. University of California Press, Berkley, CA, USA, pp. 475–488.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.
Hutchison, V.H., Maness, J.D., 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. American Zoologist 19, 367–384.
Klebenow, D.A., Gray, G.M., 1968. Food habits of juvenile sage grouse. Journal of Range Management 21, 80–83.
Klebenow, D.A., 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33, 649–662.
Knick, S.T., Hanser, S.E., Preston, K.L, 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, USA. Ecology & Evolution 3, 1539–1551.
Larsen, F.W., Bladt, J., Balmford, A., Rahbek, C., 2012. Birds as biodiversity surrogates: will supplementing birds with other taxa improve effectiveness? Journal of Applied Ecology 49, 349–356.
Lassueur, T., Joost, S., Randin, C.F., 2006. Very high resolution digital elevation models: do they improve models of plant species distribution? Ecological Modelling 198, 139–153.
Lee, J.E., Larsen, R.T., Flinders, J.T., Eggett, D.L., 2010. Daily and seasonal patterns of activity at pygmy rabbit burrows in Utah. Western North American Naturalist 70, 189–198.
Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I., McCarthy, M.A., 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology 16, 338–345.
Lentini, P.E., Wintle, B.A., 2015. Spatial conservation priorities are highly sensitive to choice of biodiversity surrogates and species distribution model type. Ecography 38, 1101–1111.
Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.
Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data. Ecology and Evolution 6, 337–348.
McMahon, L.A., Rachlow, J.L., Shipley, L.A., Forbey, J.S., Johnson, T.R, 2017. Habitat selection differs across hierarchical behaviors: selection of patches and intensity of patch use. Ecosphere 8 (11), e01993.
Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.
Merow, C., Smith, M.J., Edwards Jr., T.C., Guisan, A., McMahon, S.M., Normand, S., Thuiller, W., Wüest, R.O., Zimmermann, N.E., Elith, J, 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography 37, 1267–1281.
Milling, C.R., Rachlow, J.L., Chappell, M.A., Camp, M.J., Johnson, T.R., Shipley, L.A., Paul, D.R., Forbey, J.S., 2018. Seasonal temperature acclimatization in a semi–fossorial mammal and the role of burrows as thermal refuges. PeerJ 6, e4511.
Milling, C.R., Rachlow, J.L., Johnson, T.R., Forbey, J.S., Shipley, L.A., 2017. Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal. Behavioral Ecology 28, 1236–1247.
Natureserve, 2020. NatureServe Web Service Arlington, VA, USAAvailable at: http://www.services.natureserve.org.
Odling-Smee, F.J., Laland, K.N., Feldman, M.W., 2003. Niche construction: the neglected process in evolution. Monographs in Population Biology 37 Princeton, NJ, USA: Princeton University Press. 488 pages.
Parsons, M.A., Barkley, T.C., Rachlow, J.L., Johnson-Maynard, J., Johnson, T.R., Milling, C., Hammel, J., Leslie, I, 2016. Cumulative effects of an herbivorous ecosystem engineer in a heterogeneous landscape. Ecosphere 7, e01334.
Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017a. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893.

Phillips, S. J., Dudík, M., and Schapire, R. E. 2017b. Maxent software for modeling species niches and distributions (version 3.4.1). Available at: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed 15 May 2018.

Pierce, J.E., Larsen, R.T., Flinders, J.T., Whiting, J.C., 2011. Fragmentation of sagebrush communities: does an increase in habitat edge impact pygmy rabbits? Animal Conservation 14, 314–321.

Pilliod, D.S., Jeffries, M.I., Arkle, R.S., Olson, D.H., 2020. Reptiles under the conservation umbrella of the greater sage-grouse. Journal of Wildlife Management 84, 478–491.

PRISM Climate Group. 2012. 30-Year Normal Monthly Climate Data, 1981–2010 (800m). Available at: http://www.prism.oregonstate.edu/. Accessed 15 March 2017.

R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Accessed 22 August 2019.

Radosavljevic, A., Anderson, R.P, 2013. Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41, 629–643.

Remington, T.E., Braun, C.E., 1985. Sage grouse food selection in winter, North Park, Colorado. Journal of Wildlife Management 49, 1055–1061.

Roberge, J.M., Angelstam, P, 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18, 76–85.

Roberts, H.B., 2001. Survey of pygmy rabbit distribution, numbers and habitat use in Lemhi and Custer counties. Bureau of Land Management, Idaho State Office, Idaho. Boise, ID, USA.

Rowland, M.M., Wisdom, M.J., Suring, L.H., Meinke, C.W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129, 323–335.

Runge, C.A., Withey, J.C., Naugle, D.E., Fargione, J.E., Helmstedt, K.J., Larsen, A.E., Martinuzzi, S., Tack, J.D., 2019. Single species conservation as an umbrella for management of landscape threats. PLoS ONE 14 (1), e0209619.

Sanchez, D.M., Rachlow, J.L., 2008. Spatio-temporal factors shaping diurnal space use by pygmy rabbits. Journal of Wildlife Management 72, 1304–1310.

Schoener, T.W., 1968. Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.

Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Deibert, P.A., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V., Stiver, S.J., 2004. Distribution of sage-grouse in North America. The Condor 106, 363–376.

Searcy, C.A., Shaffer, H.B., 2016. Do ecological niche models accurately identify climatic determinants of species ranges? The American Naturalist 187, 423–435.

Shipley, L.A., Davila, T.B., Thines, N.J., Elias, B.A., 2006. Nutritional requirements and diet choices of the pygmy rabbit *(Brachylagus idahoensis):* a sagebrush specialist. Journal of Chemical Ecology 32, 2455–2474.

Suter, W., Graf, R.F., Hess, R., 2002. Capercaillie *(Tetrao urogallus)* and avian biodiversity: testing the umbrella-species concept. Conservation Biology 16, 778–788.

Smith, A.B., 2019. enmSdm: Tools for modeling species niches and distributions R package version 0.3.4.6. Available at https://www.github.com/adamlilith/enmSdm.

Smith, I.T., Rachlow, J.L., Svancara, L.K., McMahon, L.A., Knetter, S.J., 2019. Habitat specialists as conservation umbrellas: do areas managed for greater sage-grouse also protect pygmy rabbits? Ecosphere 10 (8), e02827.

Stanton, J.C., Pearson, R.G., Horning, N., Ersts, P., Reşit Akçakaya, H., 2012. Combining static and dynamic variables in species distribution models under climate change. Methods in Ecology & Evolution 3, 349–357.

Timmer, J.M., Aldridge, C.L., Fernández-Giménez, M.E., 2019. Managing for multiple species: greater sage-grouse and sagebrush songbirds. Journal of Wildlife Management 83, 1043–1056.

Steven J. Phillips, Miroslav Dudík, Robert E. Schapire. [Internet] Maxent software for modeling species niches and distributions (Version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on DATE. Accessed 15 March 2017.

Tulloch, A.I., Chadès, I., Dujardin, Y., Westgate, M.J., Lane, P.W., Lindenmayer, D., 2016. Dynamic species co-occurrence networks require dynamic biodiversity surrogates. Ecography 39, 1185–1196.

US Geological Survey (USGS), 2014. NLCD 2011 Land Cover (2011 edition, amended 2014)–National Geospatial Data Asset (NGDA) Land Use Land Cover. Raster Digital Data Set. Sioux Falls (SD): US Geological Survey Available at: https://www.mrlc.gov.

US Geological Survey (USGS), 2016a. Provisional Remote Sensing Shrub/Grass NLCD Products for the Great Basin. Raster Digital Data Set. Sioux Falls (SD): US Geological Survey Available at: https://www.mrlc.gov.

US Geological Survey (USGS), 2016b. NLCD 2011 USFS percent tree canopy (analytical version). Raster Digital Data Set. US Geological Survey, Sioux Falls, SD, USA Available at: https://www.mrlc.gov.

US Geological Survey (USGS), 2016c. eMODIS COMPOSITE NDVI version 5. Raster digital data set. Sioux Falls (SD): US Geological Survey Available at: https://earthexplorer.usgs.gov/.

US Geological Survey (USGS), 2017a. Provisional remote sensing shrub/grass NLCD products for the Montana/Wyoming area. Raster digital data set. Sioux Falls (SD): US Geological Survey Available at: https://www.mrlc.gov.

US Geological Survey (USGS), 2017b. 1 Arc-second Digital Elevation Models (DEMs)–USGS National Map 3DEP Downloadable Data Collection. Raster Digital Data Set Available at https://nationalmap.gov/3DEP/. Accessed 17 May 2016.

Ulappa, A.C., Kelsey, R.G., Frye, G.G., Rachlow, J.L., Shipley, L.A., Bond, L., Pu, X., Forbey, J.S., 2014. Plant proteins and secondary metabolites influence diet selection in a mammalian specialist herbivore. Journal of Mammalogy 95, 834–842.

Wallestad, R., Eng, R.L., 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39, 628–630.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution: International Journal of Organic Evolution 62, 2868–2883.

Warren, D., Dinnage, R., 2020. ENMTools: analysis of niche evolution using niche and distribution models R package version 1.0.1. Available at https://CRAN.R-project.org/package=ENMTools. Accessed 22 August 2019.

Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33, 607–611.

Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection. Ecological Applications 21, 335–342.

Weiss, A., 2001. Topographic position and landforms analysis, 200. ESRI, San Diego, CA, USA Poster presentation, ESRI user conference. 9-13 July 2001.

Weiss, N.T., Verts, B.J., 1984. Habitat and distribution of pygmy rabbits *(Sylvilagus idahoensis)* in Oregon. Great Basin Naturalist 44, 563–571.

Wiens, J.A., 2009. Landscape ecology as a foundation for sustainable conservation. Landscape Ecology 24, 1053–1065.

Winward, A.H., 1980. Taxonomy and ecology of sagebrush in Oregon. Agricultural Experimental Station—Oregon State University, Corvallis, OR, USA, p. 642 Station Bulletin.

Wright, A.N., Hijmans, R.J., Schwartz, M.W., Shaffer, H.B., 2015. Multiple sources of uncertainty affect metrics for ranking conservation risk under climate change. Diversity and Distributions 21, 111–122.