Annotated Bibliography of Research Focused on 1st-3rd Order Pygmy Rabbit (*Brachylagus idahoensis*) Habitat Selection

by

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ABSTRACT OF THE PROJECT OF

Emily D. Jencso for the degree of Professional Science Masters in Fish and Wildlife Administration presented on May 19, 2022. Title: Annotated Bibliography of Research Focused on 1st-3rd Order Pygmy Rabbit (*Brachylagus idahoensis*) Habitat Selection

Wildlife managers often use species distribution models (SDMs) as an initial tool in conservation planning. Managers and researchers have made efforts to model the habitat and distribution of pygmy rabbits (*Brachylagus idahoensis*) across their historic range since the species was proposed for listing under the Endangered Species Act (USFWS 2003). Pygmy rabbits are sagebrush-obligates patchily distributed across the western United States (Green and Flinders 1980). Habitat relationships for habitat specialists like the pygmy rabbit are believed to be relatively consistent throughout their geographic range. However, appropriate spatial and temporal environmental variables at local, regional, and range-wide scales are often overlooked (Wheatley and Johnson 2009, McGarigal et al. 2016). Numerous regional and range-wide pygmy rabbit distribution models have been developed using various methodologies, environmental variables, and thresholds, resulting in predictive distribution maps that range in accuracy and usefulness. Environmental variables, such as climate or vegetation, limit species distributions at broad spatial and temporal scales (1st and 2nd order selection) (Johnson 1980). In contrast, fine-scale resource selection (3rd and 4th order) tends to be limited by local community interactions (e.g., forage availability, dispersal, predation, and competition) (Johnson 1980). For instance, the species distribution of the pygmy rabbit appears to be limited by climate, phenology, soils, and vegetation at the landscape or range-wide scale (Smith et al. 2021). Whereas dispersal, predation, and specific vegetation and soil characteristics drive resource selection at finer scales (3rd and 4th order). Integrating relevant scientific research into future pygmy rabbit modeling efforts can assist wildlife managers in focusing conservation efforts. To assist in future modeling and conservation efforts focused on pygmy rabbits, I created an annotated bibliography focused on 1^{st} through 3^{rd} order habitat selection. I framed the initial search using established methods utilized by the U.S. Geological Survey (USGS) (Carter et al. 2018, 2020, Kleist 2022), and then narrowed my results to include research focused on previous modeling efforts, and 1^{st} through 3^{rd} order habitat selection. The initial search results included over 2,000 products, which were then narrowed down to 41 peer-reviewed journal articles or technical reports. I summarized each product, focusing on habitat selection and environmental variables that could be modeled at a 30 m or greater scale. I also compiled a list of published pygmy rabbit SDMs and habitat models, the broad category of environmental variables modeled (Table 1), potential data sources, and available resolution of environmental variables used in future modeling efforts (Table 4).

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ABSTRACT

Wildlife managers often use species distribution models (SDMs) as an initial tool in conservation planning. Managers and researchers have made efforts to model the habitat and distribution of pygmy rabbits (*Brachylagus idahoensis*) across their historic range since the species was proposed for listing under the Endangered Species Act (USFWS 2003). Pygmy rabbits are sagebrush-obligates patchily distributed across the western United States (Green and Flinders 1980). Habitat relationships for habitat specialists like the pygmy rabbit are believed to be relatively consistent throughout their geographic range. However, appropriate spatial and temporal environmental variables at local, regional, and range-wide scales are often overlooked (Wheatley and Johnson 2009, McGarigal et al. 2016). Numerous regional and range-wide pygmy rabbit distribution models have been developed using various methodologies, environmental variables, and thresholds, resulting in predictive distribution maps that range in accuracy and usefulness. Environmental variables, such as climate or vegetation, limit species distributions at broad spatial and temporal scales (1st and 2nd order selection) (Johnson 1980). In contrast, fine-scale resource selection (3rd and 4th order) tends to be limited by local community interactions (e.g., forage availability, dispersal, predation, and competition) (Johnson 1980). For instance, the species distribution of the pygmy rabbit appears to be limited by climate, phenology, soils, and vegetation at the landscape or range-wide scale (Smith et al. 2021). Whereas dispersal, predation, and specific vegetation and soil characteristics drive resource selection at finer scales (3rd and 4th order). Integrating relevant scientific research into future pygmy rabbit modeling efforts can assist wildlife managers in focusing conservation efforts. To assist in future modeling and conservation efforts focused on pygmy rabbits, I created an annotated bibliography focused on 1^{st} through 3^{rd} order habitat selection. I framed the initial search using established methods utilized by the U.S. Geological Survey (USGS) (Carter et al. 2018, 2020, Kleist 2022), and then narrowed my results to include research focused on previous modeling efforts, and 1st through 3rd order habitat selection. The initial search results included over 2,000 products, which were then narrowed down to 41 peer-reviewed journal articles or technical reports. I summarized each product, focusing on habitat selection and environmental variables that could be modeled at a 30 m or greater scale. I also compiled a list of published pygmy rabbit SDMs and habitat models, the broad category of environmental variables modeled (Table 1), potential data sources, and available resolution of environmental variables used in future modeling efforts (Table 4).

KEYWORDS Annotated bibliography, pygmy rabbit, *Brachylagus idahoensis*, habitat model, habitat selection, sagebrush obligate, species distribution model.

INTRODUCTION

Pygmy rabbits (*Brachylagus idahoensis*) are sagebrush obligates, patchily distributed throughout sagebrush ecosystems within the Great Basin and adjacent intermountain west (Green and Flinders 1980, Weiss and Verts 1984). They primarily occupy areas of tall, dense sagebrush with loose soils appropriate for digging burrows (Green and Flinders 1980, Weiss and Verts 1984, Katzner and Parker 1997a). The spatial extent of sagebrush-steppe ecosystems has decreased an estimated 40-50% since Euro-American settlement (Connelly and Clait 1997, West and Young. 2000, Connelly et al. 2004, Schroeder et al. 2004, Xian et al. 2012). Remaining intact sagebrush areas are considered one of the most at-risk ecosystems in North America (Noss et al. 1995, Mackey 2003, Miller 2010). As a result, species dependent on sagebrush ecosystems have experienced substantial range contractions and population declines (Dobkin and Sauder. 2004)

The pygmy rabbit is a species of greatest conservation need or concern across its range (NatureServe 2022). It was petitioned for federal listing under the Endangered Species Act (ESA) of 1973 in 2003 due to the loss of sagebrush habitat within its historical geographic range (Committee for the High Desert et al. 2003). The petition cited overgrazing, fire, vegetation manipulation, energy development, off-highway vehicle use, and agricultural and urban development as threats facing the species (Committee for the High Desert et al. 2003). A distinct population segment of pygmy rabbits in the Columbia Basin in Washington was listed as endangered under the ESA (U.S. Fish and Wildlife Service 2003). However, the U.S. Fish and Wildlife Service (hereafter, "the Service or USFWS") determined the species did not warrant federal protection citing insufficient data on pygmy rabbit populations across its range to determine whether substantial range-wide declines were occurring (U.S. Fish and Wildlife Service 2010). The determination also suggested pygmy rabbits still existed across their historical range in portions of California, Nevada, Oregon, Idaho, Utah, Wyoming, Montana, and Washington (U.S. Fish and Wildlife Service 2010). Additionally, the Service concluded that the available information did not indicate pygmy rabbits are significantly impacted by "sagebrush loss or modification from various actions, hunting, research activities, predation, disease, or inadequacies of existing regulatory mechanisms across its range (U.S. Fish and Wildlife Service 2010)." There has been considerable research published since the Service's 2010 Not Warranted Decision.

Habitat Selection and Species Distribution Models

Wildlife managers often utilize species distribution models (SDMs) as an essential first step in conservation planning for rare species (Rachlow and Svancara 2006). Rare species offer unique challenges to researchers and wildlife managers attempting to study and manage their populations (Karl et al. 1999, Rachlow and Svancara 2006). For instance, rare species may be furtive or have life-history strategies that reduce detectability, leading to inaccurate estimates of distribution or abundance (Flather and Sieg 2007). Consideration of species-appropriate temporal and spatial scales may prevent under or overestimating distribution or abundance when modeling species distributions. A concern about SDMs is that they often overpredict species distribution of rare species with predicted distributions clustered around known locations (Baldwin 2009). Additionally, many species select different habitat components at multiple scales (Johnson 1980, Bergin 1997, Apps and McLellan 2001, Johnson et al. 2002, Mayor et al. 2009). Modeled environmental variables may not be of a scale relevant to the species being studied, and SDMs often assume a population to be at equilibrium in both time and space (Bean et al. 2014). Ecologists have widely adopted a hierarchical multi-scale habitat selection framework (Johnson 1980). Within this framework, spatial and temporal scale differences between resource selection levels (1^{st} order = physical or geographical range of a species; 2nd order = home range of an individual or social group; 3rd order = habitat patches within a home range; and 4th order = specific resources within a habitat patch) have become implicit rather than explicit (Mayor et al. 2009, McGarigal et al. 2016). Biologically relevant scales are infrequently considered when selecting environmental variables to be evaluated against species response within a multi-scale habitat framework (Wheatley and Johnson 2009, McGarigal et al. 2016). Environmental variables, such as climate or vegetation, limit species distributions at broad spatial and temporal scales (1^{st} and 2^{nd} order). In contrast, fine-scale resource selection (3^{rd} and 4^{th} order) tends to be limited by local community interactions (e.g., forage availability, dispersal, predation, and competition). For instance, the species distribution of the pygmy rabbit appears to be limited by climate, phenology, soils, and vegetation at the landscape or range-wide scale (Smith et al. 2021). Whereas dispersal, predation, and as specific vegetation and soil characteristics are drivers of resource selection at finer scales (3rd and 4th order).

Excepting Arizona, Colorado, and Utah, the distribution of pygmy rabbits has been modeled in states where they occur. Efforts to model the availability and distribution of potential habitat have been met with minimal success. Keinath and McGee (2004) suggest such modeling efforts are primarily useful for focusing future survey efforts. The coarse resolution of model inputs, different grain sizes for environmental variables, and lack of absence data have been identified as potentially problematic in previous pygmy rabbit SDMs (Lenard et al. 2005, Meisel et al. 2006). Additionally, models that used only existing presence data from natural history collections may not have accounted for bias within these datasets. For instance, clusters of points from natural history datasets are typically a result of intensive local efforts, introducing sampling bias. Advances in species distribution modeling provide potential solutions to problems associated with conceptualization, data preparation, model fitting, and evaluation phases, including sampling bias (Guisan et al. 2005).

Pygmy rabbit SDMs have been developed using environmental variables in Wyoming (Keinath and McGee 2004, The Nature Conservancy of Wyoming 2004, Germaine et al. 2014), Montana (Lenard et al. 2005, Burkholder 2016), Idaho (Gabler and Laundre 2000, Gabler et al. 2001, Simons and Laundre 2004, Rachlow and Svancara 2006), Nevada (Himes and Drohan 2007, Larrucea and Brussard 2008a), California (Larrucea and Brussard 2008a), and Washington (Meisel et al. 2006). Environmental variables used as model inputs and model accuracy in predicting potential habitat varied (Table 1). Vegetation, soils, and elevation were included as variables in most of the models (Table 1). Many of these models lacked high-resolution vegetation and detailed soil data, which likely impacted performance. Additionally, pygmy rabbits do not occupy all patches of habitable vegetation throughout the landscape, likely due to population-level effects (i.e., predation, disease, competition) (Gabler and Laundre 2000, Germaine et al. 2014).

In 2019 an inductive range-wide species distribution model for the pygmy rabbit was developed using state and federal occurrence data and home range information (Smith et al. 2019). This model was the first range-wide SDM for the species built at a 30-m resolution. However, the model was not field validated and relied on uneven survey effort throughout the species range. The range-wide pygmy rabbit model (Smith et al. 2019) predicts large areas of potential habitat where no occurrence data exists, suggesting a tradeoff between model specificity and generality due to the broad extent of the modeling effort (Elith and Leathwick 2009, Rush 2021). Smith et al. (2019) also estimated overlap between modeled range-wide pygmy rabbit habitat with greater sage-grouse habitat management areas (HMAs). They suggested that priority and general sage-grouse HMAs encompass 59% and 34%, respectively, of primary habitat for pygmy rabbits (Smith et al. 2019). Federal and state actions and policies within sage-grouse HMAs are suggested to confer protection to sagebrush steppe species like the pygmy rabbit under a conservation umbrella (BLM and USFS 2015). Comparing range-wide overlap between sage-grouse and pygmy rabbits can be problematic due to variation in space and habitat use between the species, both spatially and temporally. Regional distributions for pygmy rabbit and sage-grouse have less overlap than suggested by the range-wide model (Smith et al. 2021). Local and regional habitat modeling in Idaho comparing pygmy rabbit and sage-grouse overlap was lower (49% overlap) than the range-wide model and even lower when seasonal habitat was considered (18-31%) (Smith et al. 2021). Range-wide distribution models for a cryptic species like the pygmy rabbit that rely on broad spatial scales and occurrence only data are unlikely to capture regional variation in available habitat and intraspecific niche variation. The environmental variables that influence habitat selection will differ at range-wide versus regional and local scales. Similarly, habitat characteristics identified as important through resource selection functions may not be identified as an influential variable in an SDM. For instance, when comparing regional models in Idaho, researchers found that sagebrush cover was an important variable in only two out of five models (Rush 2021). In contrast, bioclimatic variables were a stronger predictor of species distribution than sagebrush cover (Rush 2021).

Managers often use species distribution models as an initial step to identify areas of potential habitat and focus survey efforts. Teasing out environmental variables and associated thresholds to be used in the modeling process should be done with considerable thought to maximize the usefulness of regional models. This document is meant to provide wildlife managers working with pygmy rabbits with a repository of existing peer-reviewed research published between 1980-2021 focused on pygmy rabbit habitat selection and modeling efforts. The resulting annotated bibliography is intended to complement the US Geologic Survey's (USGS) recent Open File Report 2022-1003: Annotated Bibliography of Scientific Research on Pygmy Rabbits Published from 1990 to 2020 (Kleist et al. 2022). The USGS bibliography summarizes scientific research on pygmy rabbits from 1990 to 2020. This document further examines research focused on pygmy rabbit habitat selection and environmental variables that researchers could use in future species distribution models.

METHODS

Numerous reports (e.g., Carter et al. 2018, 2020, Kleist 2022) introduced a standardized methodology for conducting research reviews to facilitate the integration of recent, peer-reviewed science into resource management decisions (Kleist 2022). I have utilized these methods to structure the preliminary portion of the research review that follows to support future local or regional pygmy rabbit modeling efforts by researchers or managers.

I conducted an initial structured search of three reference databases—Web of Science, Science Direct (accessed through the Oregon State Library), and Google Scholar (accessed through Harzing's Publish or Perish) —using the search term "pygmy rabbit" on August 15, 2021. A subsequent search was conducted on January 15, 2022. The search returned all items containing the search term in the product title, abstract, keywords, main text, or references.

I then refined the resulting list of products in four ways. First, I removed duplicate items. Second, I retained only those articles with the phrase "pygmy rabbit" present in the article title, abstract, or author-supplied keywords (when available) or in the main text to ensure that the article was relevant. Third, I excluded products not published in peer-reviewed journals or as formal technical reports. Fourth, I excluded editorial content (such as policy perspectives and commentaries), reports without evidence of a formal peer-review process (such as project and annual reports without a technical series or volume number), conference abstracts, article preprints, magazine articles, theses, dissertations, manuscripts not yet in press, and books. However, a comprehensive list of citations and weblinks of theses, dissertations, and unpublished work focused on pygmy rabbit habitat or species distribution models between 1946 and 2021 was retained and is available in Appendix B. Finally, I excluded any remaining articles or reports that, upon review, did not have content of clear relevance to the conservation and management of pygmy rabbits. For instance, papers focused on the greater sage-grouse as an umbrella species regularly mention the pygmy rabbit as an example benefitting from sage-grouse habitat protection. I excluded papers that only mention the pygmy rabbit as an example. Early research focused on pygmy rabbits was often descriptive (Green and Flinders 1980, Green and Jerran 1981) or listed survey results (Janson 1946) and thus were excluded.

The literature search resulted in 182 articles from the Web of Science, 135 from Science Direct, and 1,950 from Google Scholar. After applying the initial selection criteria (Carter et al. 2018, 2019) to remove duplicates, non-peer-reviewed research, theses, and books a total of 128 articles remained. The remaining 128 articles were then assigned a management topic based on a precursory review of the abstract and results. Management topics are listed and defined in Table 2. I refined articles classified under biogeography, habitat characteristics (site and/or broad scale), dispersal, habitat characteristics, and distribution models under hierarchal habitat selection. Articles were assigned a habitat selection category of either 1st order, 2nd order, 3rd order, 4th order (Johnson 1980), or multiple selection scales (Table 3). A total of 41 articles focused on first-through third-order habitat selection are included in this bibliography. The focus of this bibliography is on pygmy rabbit physical or geographical range (1st order), home range (2nd order), and habitat patches within a home range (3rd order). Selection of specific resources within habitat patches (4th order), such as protein analysis of foraged sagebrush, are beyond parameters that can be modeled at a spatial scale of 30 meters or more and therefore not included.

I then summarized the contents of each product with a focus on habitat selection and potential model covariates. Additionally, I assessed the content of each article relevant to a list of potential model variables (Table 4) and provided available range-wide datasets for each variable (Table 5). I also noted which articles/reports have associated geospatial data or produced a species distribution or habitat model and provided a functioning weblink where available. The original product should always be consulted for detailed information.

ANNOTATED BIBLIOGRAPHY

Camp, M.J., Rachlow, J.L., Woods, B.A., Johnson, T.R., and Shipley, L.A. 2012. When to run and when to hide—The influence of concealment, visibility, and proximity to refugia on perceptions of risk: Ethology, v. 118, no. 10, p. 1010–1017.

https://doi.org/10.1111/eth.12000

The authors suggest that higher levels of visibility influenced the perception of risk in pygmy rabbits, regardless of the amount of concealment. They collared 49 pygmy rabbits at 3 study sites and relocated each animal between May and August 2010. They measured flight initiation distance (distance at which pygmy rabbits fled from researchers) as a surrogate of perceived risk and concealment and visibility conferred by vegetation at these locations. The authors found that the proximity of burrows significantly lowered flight initiation distance, and the average distance of pygmy rabbits to burrows ranged from 9 m to 67 m (n=227, SD =10.10). Concealment by vegetation decreased the perception of risk. However, as visibility increased, the relationship between perceived risk and concealment became less pronounced. Pygmy rabbits are central place foragers, restricting their movements to areas near their burrow systems (Heady and Laundre 2005, Sanchez and Rachlow 2008, Price 2009). The authors' findings suggest that vegetation structure that provides high concealment may be a strategy for avoiding predators in pygmy rabbits.

Carr, N.B., and Melcher, C.P., eds. 2017. Wyoming Basin Rapid Ecoregional Assessment: (ver. 1.1, April 2017) U.S. Geological Survey Open-File Report 2015–1155, 896 p.

https://doi.org/10.3133/ofr20151155

The authors developed a general habitat model for pygmy rabbits using MaxEnt software (Phillips et al. 2006) as part of a Rapid Ecoregional Assessment (REA) in the Wyoming Basin. Key ecological attributes addressed included the distribution of pygmy rabbit habitat, landscape structure (patch size and connectivity), landscape dynamics (fire and sagebrush-juniper ecotone shifts), and anthropogenic change agents (development and climate change). The resulting model predicted that 23,950 km^2 (13.4 %) of the Wyoming Basin was potential habitat for the species. The authors found that 20% of potential habitat in the Basin was relatively undeveloped, whereas 35% had high levels of development, corresponding to sagebrush shrubland development overall. Development has effectively fragmented pygmy rabbit habitat into smaller patches relative to baseline conditions. Only 7.8% of undeveloped areas occur in patches greater than 100 km^2 (38.6 mi^2), and there are no relatively undeveloped patches of potential habitat greater than 1,000 km^2 (386.1 mi^2). The authors found baseline pygmy rabbit habitat is highly connected, whereas development has dramatically reduced the structural connectivity of potential habitat at local, landscape, and regional scales. The authors suggest that despite interpatch distances being smaller than the maximum reported distances for dispersal (6.5 km (4.0 mi) for females and 11.9 km (7.4 mi) for males) that roads may negatively impact dispersal due to avoidance or direct mortality. Therefore, development occurring outside of these patches may still impede pygmy rabbit dispersal.

Crowell, M.M., Shipley, L.A., Camp, M.J., Rachlow, J.L., Forbey, J.S., and Johnson, T.R. 2016. Selection of food patches by sympatric herbivores in response to concealment and distance from a refuge: Ecology and Evolution, v. 6, no. 9, p. 2865–2876.

https://doi.org/10.1002/ece3.1940

Crowell et al. (2016) examined differences in forage patch selection between mountain cottontails and pygmy rabbits by comparing concealment cover, cover orientation, and proximity to burrows. The authors conducted three feeding trials with food patches varying in percent cover of either terrestrial or aerial concealment and distances from refuge. Models were used to examine the effects of orientation and amount of concealment, and distance to refuge on forage patch selection. Both species preferred patches with higher cover. Pygmy rabbits preferred patches with greater terrestrial cover, whereas cottontails preferred patches with higher aerial cover. Additionally, pygmy rabbits selected food patches closer to a burrow refuge, whereas the distance to burrows did not affect forage patch selection in cottontails. The authors suggest that these two species' life-history traits influence habitat use to lower predation risk. Pygmy rabbits' small size may influence their reliance on burrows to avoid predation, while cottontails prefer to run away. Pygmy rabbits may be more susceptible to terrestrial predators that excavate their burrows, explaining their preference for terrestrial cover. Crowell et al. (2016) further suggest that habitat alterations may impact these species differently based on niche partitioning.

Edgel, R. J., R. T. Larsen, J. C. Whiting, and B. R. McMillan. 2018. Space use, movements, and survival of pygmy rabbits in response to construction of a large pipeline. Wildlife Society Bulletin 42:488-497. https://doi.org/10.1002/wsb.908

The authors quantified space use, movements, and survival of pygmy rabbits before and after the construction of an oil pipeline right-of-way in Utah over 18 months. They captured and radiomarked 108 pygmy rabbits at a control site and the pipeline and documented their locations multiple times a day for a month before and after pipeline construction. Location data was then recorded three to four times a week in the summer and biweekly from September to April. The authors then estimated each rabbit's home ranges and core areas and modeled space use and movements. Pygmy rabbit home ranges and core areas were three times larger before construction of the pipeline and core areas shifted away from the pipeline and remained smaller post-construction. Survival rates between the pipeline construction site and control site did not differ significantly. Only 3 of 22 rabbits crossed the right-of-way after construction. The authors suggest that energy development results in habitat loss and decreases space use by pygmy rabbits, therefore reducing presence and abundance. Furthermore, the authors suggest that avoidance behavior of edge habitats likely explains the observed decrease in home ranges and core areas, which may increase competition and reduce gene flow.

Edgel, R.J., Pierce, J.L., and Larsen, R.T. 2014 Pygmy rabbit (*Brachylagus idahoensis*) habitat selection—Does sagebrush (*Artemisia* spp.) age influence selection? Western North American Naturalist, v. 74, no. 2, p. 145−154. https://doi.org/10.3398/064.074.0201

The authors sought to describe site-specific habitat characteristics of habitat occupied by pygmy rabbits and determine if sagebrush age was a meaningful indicator of site-scale habitat selection in Utah. They sampled 77 habitat variables at occupied (n=72) and unoccupied (n=61) sites for a statewide pygmy rabbit survey. Occupied sites had greater horizontal obscurity (cover), occurred at higher elevations, had greater percent understory cover composed of sagebrush and other shrubs, and less sagebrush decadence than unoccupied sites. Sagebrush age did not appear to be an important variable when compared between occupied and unoccupied sites.

Estes-Zumpf, W.A., and Rachlow, J.L. 2009. Natal dispersal by pygmy rabbits (*Brachylagus idahoensis*): Journal of Mammalogy, v. 90, no. 2, p. 363–372. https://doi.org/10.1644/08-MAMM-A-078.1

Estes-Zumpf and Rachlow used radiotelemetry to investigate the dispersal patterns and capabilities of pygmy rabbits in east-central Idaho. They also sought to determine the effects of social and environmental factors on natal dispersal of both males and females. The authors tagged 61 juvenile rabbits from May to July 2004 and 2005 at three study sites. These data were then used in a spatial analysis to model the effect of sex, study year, date of emergence, and body condition on dispersal frequency and distance and the effect of rabbit burrow density on dispersal frequency and distance. Both males and females displayed high rates of dispersal (males=90%, females =80%), with juvenile females dispersing three times farther than males. Average natal dispersal distances were 1.0 km (range = 0.03-6.5 km) and 2.9 km (range =0.02-11.9 km) for males and females, respectively. Dispersing juveniles crossed gravel roads and perennial streams; however, they initiated dispersal away from streams. Pygmy rabbits dispersed rapidly as one-way movements through unfamiliar areas and rarely made exploratory visits prior to dispersal. Mortality rates for male and female juvenile rabbits were 69.2% and 88.5%, respectively, with avian predation being the most common cause of mortality.

Estes-Zumpf, W.A., Rachlow, J.L., Waits, L.P., and Warheit, K.I. 2010. Dispersal, gene flow, and population genetic structure in the pygmy rabbit (*Brachylagus idahoensis*): Journal of Mammalogy, v. 91, no. 1, p. 208–219. . https://www.doi.org/10.1644/09-MAMM-A-032R.1

The authors examined gene flow, genetic diversity, and population genetic structure and investigated the effects of barriers (secondary roads, highways, creeks, and agriculture pastures) on pygmy rabbits in Idaho. Genetic samples were taken from pygmy rabbits at two study sites. Researchers then conducted genetic analyses to determine if dispersal differed by sex. The authors found high levels of diversity at both sites and no evidence of sex-biased dispersal or isolation by distance at either site. Low levels of roads and streams in the study area did not appear to inhibit gene flow. However, agricultural development may increase isolation and inhibit gene flow between populations.

Estes-Zumpf, W.A., Zumpf, S.E., Rachlow, J.L., Adams, J.R., and Waits, L.P. 2014. Genetic evidence confirms the presence of pygmy rabbits in Colorado: Journal of Fish and Wildlife Management, v. 5, no. 1, p. 118–123. 118–123. https://doi.org/10.3996/012013-JFWM-005R

Estes-Zumpf et al. (2014) presented the first known evidence of pygmy rabbits in Colorado. The authors collected and analyzed fecal pellets from the Vermillion Bluffs area of northwestern Colorado. Laboratory analysis verified all the pellets samples as pygmy rabbits. The density of pygmy rabbits in the study area appeared low based on the sparseness of pellets. The authors suggest that further assessment of the conservation status of pygmy rabbits in Colorado is warranted based on their findings.

Gabler, K.I., Laundré, J.W., and Heady, L.T. 2000. Predicting the suitability of habitat in southeast Idaho for pygmy rabbits: The Journal of Wildlife Management, v. 64, no. 3, p. 759–764. .https://doi.org/10.2307/3802746

Gabler et al. (2000) developed a predictive GIS model in southeastern Idaho to determine the percent remaining suitable pygmy rabbit habitat. The authors conducted a spatial analysis using environmental variables (vegetation, surface geology, slope, and aspect) overlaid with burrow locations to determine local ecological conditions that support burrows. Covariate thresholds were determined using local knowledge of pygmy rabbit habitat use. Gabler and Laundre (2000) evaluated model accuracy through field validation of presence/absence surveys at randomly selected sites. The model successfully predicted areas not occupied (100% accurate) and 57% occupied. The authors suggest the model may be a useful first step in identifying appropriate habitat, potentially throughout the range. The coarse-scale of available vegetation layers was a limiting factor in predicting use areas. Gabler et al. (2000) could not distinguish between sites with little to no sagebrush cover versus areas with a higher percentage of sagebrush cover because functional groups rather than cover classes made up the vegetation layer. The authors also suggest incorporating fire history and cheatgrass layers into future models to increase accuracy. Additionally, temporal variability in climate over 7 to 9 years could cause significant changes within a local patch of vegetation (Anderson et al. 1996), therefore, layers used for analysis should be spatially and temporally relevant.

Gabler, K.I., Heady, L.T., and Laundré, J.W. 2001. A habitat suitability model for pygmy rabbits (*Brachylagus idahoensis*) in southeastern Idaho: Western North American Naturalist, v. 61, no. 4, p. 480–489. https://jstor.org/stable/41717145

Gabler et al. (2001) sought to develop a habitat suitability model for pygmy rabbits at the Idaho National Engineering and Environmental Laboratory (INEEL) in southeastern Idaho. They measured habitat characteristics at burrow sites, unoccupied burrow sites, inactive areas, and nonuse areas and then conducted a principal components analysis of seventeen vegetation variables and soil texture. Ten vegetation variables accounted for 63% of the variation in plots, six of which differed significantly among plot types in a univariate analysis. Modeled suitable pygmy rabbit habitat was best characterized by greater shrub and forb cover and shrub density (including big sagebrush). Additionally, nonuse areas had less sandy soils with more silt and clay. The authors suggest that pygmy rabbits select burrow locations on a finer scale than previously thought or modify their habitat near their burrow locations through site selection.

Germaine, S., Ignizio, D., Keinath, D., and Copeland, H. 2014. Predicting occupancy for pygmy rabbits in Wyoming—An independent evaluation of two species distribution models: Journal of Fish and Wildlife Management, v. 5, no. 2, p. 298–314. https://doi.org/10.3996/022014-JFWM-016

Germaine et al. (2014) evaluated the classification accuracy of two species distribution models in Wyoming. The Nature Conservancy (TNC) developed the first model based on expert opinion and published research, and the Wyoming Natural Diversity Database (WNDD) developed the second model using a maximum entropy algorithm and historical observation data. The WNDD selected 18 environmental covariates based on published literature and exploratory analyses of occurrence data. Then the WNDD used raster data to produce a binary map based on landscape characteristics in a geographic information system. In contrast, TNC used knowledge of pygmy rabbit habitat preferences to establish a range of values for six environmental covariates. The TNC researchers then used a focal mean function to smooth the model to a 30-m resolution. Germaine et al. (2014) independently evaluated each of these pygmy rabbit habitat models using 187 survey points throughout southwestern Wyoming. Both models were better at predicting occupied habitat than nonhabitat. The overall classification success for the TNC model was 63.3% and 61.2% for the WNDD model. However, the models were not harmonious in classifying 41.9% of the study area. Germaine et al. (2014) found that both models' classification success declined as road density increased beyond 5 km roads/ per km^2. The authors suggest wildlife managers use the two models concurrently when evaluating areas as habitat or nonhabitat and place more confidence in pixels that align in habitat classification and validating areas on the ground in areas of higher anthropogenic use.

Germaine et al. 2017. Relationships between gas field development and the presence and abundance of pygmy rabbits in southwestern Wyoming. Ecosphere 8:e01817.

https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1817

The authors sought to 1) understand the relationship between gas field development and pygmy rabbit presence and abundance, 2) identify thresholds of disturbance where pygmy rabbit presence may decline significantly, and 3) consider whether surface disturbance limits in place for greater sage-grouse confer effective conservation for pygmy rabbits. A total of 120 plots across four gas fields were surveyed for pygmy rabbit presence for two consecutive seasons between 2011 and 2013. Germaine et al. (2017) then mapped and quantified surface disturbance from gas infrastructure and measured total sagebrush and shrub cover using a high-resolution map of rangeland vegetative cover types (Homer et al. 2009). The authors then modeled the relationship between gas field elements, pygmy rabbit presence, and two indices of pygmy rabbit abundance. They found that gas field infrastructure, specifically buried utility corridors, gas well pad complexes, adjacent disturbed areas, and well pad access roads, were negatively correlated with pygmy rabbit abundance. Pygmy rabbit presence and abundance declined sharply after

approximately 2% of the area was utilized for gas infrastructure. The authors concluded that pygmy rabbits are sensitive to gas field development, and populations may decline significantly at a threshold lower than allowed through greater sage-grouse planning and policy documents.
Associated dataset: Germaine, S.S., Carter, S.K., Ignizio, D.A., and Freeman, A.T., 2017, Analysis of land disturbance and pygmy rabbit occupancy values associated with oil and gas extraction in southwestern Wyoming (June 7, 2012): U.S. Geological Survey data release. https://doi.org/10.5066/F7BR8QDD

Germaine, S.S., Assal, T., Freeman, A., and Carter, S.K. 2020. Distance effects of gas field infrastructure on pygmy rabbits in southwestern Wyoming: Ecosphere, v. 11, no. 8, article e03230, 16 p. https://doi.org/10.1002/ecs2.3230

The authors evaluated the relationship between the distance of gas infrastructure to pygmy rabbit presence and abundance and whether well pads were more likely to be in areas of suitable pygmy rabbit habitat. A total of 120 plots across four gas fields were surveyed for pygmy rabbit presence for two consecutive seasons between 2011 and 2013. Then they compared the frequency of suitable pygmy rabbit habitats using an existing habitat suitability model (WGFD 2010) to a random sample of 200 well pads and generated 200 random points on gas fields. Presence and abundance data were then modeled using boosted regression trees to evaluate the relationship to distance of gas infrastructure. The authors found that the abundance and probability of pygmy rabbits presence was negatively correlated with gas infrastructure, with presence being lower 0.5-1.5 km of the nearest road and 2 km of well pads and utilities. Over 95% of undeveloped areas within one of the gas fields were within 2 km of gas infrastructure, and 82% of the surface area was within 1 km. The authors suggest that future gas fields are developed in poor wildlife habitat, and oil companies utilize directional drilling to reduce the total surface area of gas infrastructure.

Hagar, J., and Lienkaemper, G. 2007. Pygmy rabbit surveys on state lands in Oregon: U.S. Geological Survey Open-File Report 2007–1015, 23 p. https://doi.org/10.3133/ofr20071015
The authors' primary objective was to document the presence or absence of pygmy rabbits on state lands in southeast Oregon. They developed a habitat suitability model based on methods described in Rachlow and Svancara (2003) to prioritize survey areas. The authors removed areas with tree cover, without sage, or soils less than 61 cm deep from consideration. Detailed soil and vegetation data (SSURGO; USDA-NRCS 2005) were not available for the entire study area. Therefore, the authors used state soil data (STATSGO; USDA-SCS 1994) and a local sagebrush layer for spatial analysis resulting in a coarse-scale habitat suitability map. The authors classified sagebrush types from high to low suitability (high= Wyoming big sagebrush, moderate= mountain big and mountain low sage, and low = all other sagebrush). Pygmy rabbit surveys were then conducted at 157 priority sites based on the predicted habitat suitability map. A total of 18 sites were active, and 14 sites were considered inactive (sign of pygmy rabbits but burrows no longer occupied). Occupancy was positively correlated with greater average shrub cover and shrub height. The authors found that the median values for shrub cover (57%) and shrub height (86 cm) were consistent with values reported in other studies. Hagar and Lienkaemper (2007) suggested future modeling efforts are needed to identify thresholds of minimum patch size that support pygmy rabbit populations and estimate maximum inter-patch distances based on dispersal distances.

Heady, L. T., K. I. Gabler, and J. W. Laundré. 2001. Habitat selection by pygmy rabbits in southeast Idaho. Idaho Technical Bulletins 2001-007. **https://www.blm.gov/sites/blm.gov/files/documents/files/Library_Idaho_TechnicalBulletin2001-07.pdf**

Heady et al. (2001) conducted a multi-scale assessment of habitat selection by pygmy rabbits at the Idaho National Engineering and Environmental Laboratory (INEEL). A landscape-scale spatial analysis in a GIS was performed using four layers: vegetation, surface geology, slope, and aspect. The authors overlaid the results of this analysis with known pygmy rabbit burrow locations. A predictive map was produced to determine potential pygmy rabbit habitat areas and field-validated using presence and absence surveys at randomly selected sites. Biotic and abiotic characteristics were collected at randomly selected sites. Additionally, pygmy rabbit use patterns were further investigated using radio telemetry. The vegetative characteristics at burrows were measured and evaluated using a principal component analysis. Pygmy rabbits select areas dominated by big sagebrush (*Artemisia tridentata*) species and greater shrub cover at the landscape scale. Areas of high use within pygmy rabbit home ranges tended to have higher structural variability and sandy soils. While at the burrow scale, pygmy rabbits selected for a higher diversity of forbs, complex vegetation profile, and high shrub cover. The authors demonstrated that pygmy rabbits are habitat specialists across multiple scales. Heady et al. (2001) suggested that improvements in vegetation layers and cover products would improve predictive model outputs.

Heady, L.T., and Laundré, J.W. 2005. Habitat use patterns within the home range of pygmy rabbits (*Brachylagus idahoensis*) in southeastern Idaho: Western North American Naturalist, v. 65, no. 4, p. 490–500. https://jstor.org/stable/41717484

The author's objective was to examine behavioral use, vegetation, and physiographic features of summer home ranges of pygmy rabbits in southeast Idaho. They live-trapped and fitted radio collars to 11 pygmy rabbits (7 females and 4 males), which were then tracked from two fixed telemetry stations to determine patterns of home range use. Home range use patterns were estimated using the grid method (Rongstad and Tester 1969, Laundré and Keller 1984). Habitat characteristics between use areas were measured and used in a principal component analysis to determine which variables best characterized high-use, low-use, and burrow areas. The authors found that females had smaller mean home ranges than males, 37.2 and 67.9 ha, respectively. Both sexes spent a disproportionate amount of time and travel in areas within a 60-m radius of their burrows. Shrub density, specifically big sagebrush, and forb density were significantly higher near the burrow than high or low-use areas. The authors suggest pygmy rabbits are likely burrow obligates, and their affinity to their burrows may be related to predation risk. It remained unclear whether pygmy rabbits are selecting specific habitat characteristics within sagebrush habitat to burrow or whether they create these specific habitat characteristics through their behavior, such as burrowing and foraging.

Himes, J.G., and Drohan, P.J. 2007. Distribution and habitat selection of the pygmy rabbit, *Brachylagus idahoensis*, in Nevada (USA): Journal of Arid Environments, v. 68, no. 3, p. 371–382. https://doi.org/10.1016/j.jaridenv.2006.07.003

Himes and Drohan (2007) evaluated the distribution and habitat selection of the pygmy rabbit in Nevada and found the species was not as uncommon as previously thought. A model was developed in ArcGIS using observation data collected during road surveys, a 30-m digital elevation model, and soils data (1-km) from the CONUS soil database. Using digital stream coverage data, they also calculated the nearest distance to streams (perennial, intermittent) and springs from active pygmy rabbit sites. Himes and Drohan (2007) conducted a spatial analysis to compare the difference between soils, hydrology, and lithology between observation sites. The authors then used a principal component analysis to determine which variables were the most important source of habitat variation between sites with and without pygmy rabbits. The equation successfully explained the sign or presence of 57% of their observational data. Survey sites where pygmy rabbits were present were closer to perennial streams, had greater soil depth, and had more northerly aspects relative to areas where pygmy rabbits were absent.

Katzner, T.E., and Parker, K.L. 1997. Vegetative characteristics and size of home ranges used by pygmy rabbits (*Brachylagus idahoensis*) during winter: Journal of Mammalogy, v. 78, no. 4, p. 1063–1072 https://doi.org/10.2307/1383049

The authors evaluated the sizes of winter home ranges of pygmy rabbits in southwestern Wyoming and described the vegetation within and outside these areas. Pygmy rabbits were trapped and fitted with radio transmitters and relocated 1 to 3 times each day, and the authors calculated winter home ranges using the adaptive-kernel method (Swihard and Slade 1985, Swihart et al. 1998). Vegetation characteristics and snow depth were collected in high and low use areas and analyzed to determine whether pygmy rabbit use differed in response to these variables. The authors found that pygmy rabbit winter home ranges varied in size between tagged individuals and study years. 70% of pygmy rabbits used multiple core areas within their home range. Sagebrush cover, height, .and density tended to be higher in pygmy rabbit use areas compared to non-use areas. In 1993 pygmy rabbits used areas with greater snow depth than areas with less snow depth, suggesting that snow cover may lead to variation in winter home range sizes due to the benefits conferred from the subnivean environment. The authors suggest that vegetative cover influences home range size more than forage.

Katzner, T.E., and Parker, K.L. 1998. Long-distance movements from established burrow sites by pygmy rabbits (*Brachylagus idahoensis*) in southwestern Wyoming: Northwestern Naturalist, v. 79, no. 2, p. 72–74. https://doi.org/10.2307/3536706

The authors captured a long-distance movement of a single pygmy rabbit from its burrow across unsuitable habitat. Katzner and Parker conducted monthly pygmy rabbit surveys and tracked 15 radio-collared rabbits as part of a larger study on pygmy rabbit winter ecology. They observed a single male rabbit move 3.5 km over 2 days, crossing areas typically considered unsuitable habitat. The individual rabbit utilized abandoned burrows and rested and foraged in isolated sagebrush islands between movements. The authors compared vegetative characteristics at these isolated burrows to those at burrows used by non-moving rabbits and found the sagebrush at burrow sites to be similar. The authors suggest breeding behavior of male pygmy rabbits could generate long-distance movements. Additionally, the species can travel across unsuitable habitat and longer distances than previously thought. Finally, the authors suggest that populations may not be as isolated as previously thought due to potential dispersal behavior and movements.

Larrucea, E. S., and P. F. Brussard. 2008. Habitat Selection and Current Distribution of the Pygmy Rabbit in Nevada and California, USA. Journal of Mammalogy 89:691-699. **https://doi.org/10.1644/07-MAMM-A-199R.1**

Larrucea and Brussard (2008) used infrared camera traps to survey pygmy rabbits in Nevada and California to determine habitat selection and the species' current distribution. A potential map of pygmy rabbit habitat was created by conducting a landscape spatial analysis in a GIS. Environmental variables included soils (STATSGO 1:250,000), elevation (30-m USGS digital elevation model), vegetation (GAP Analysis, USGS, 1:24,000), and thresholds based on published research relating to the pygmy rabbit, in addition to spatial analysis of covariates at historic pygmy rabbit locations. The authors also investigated whether the pygmy rabbit is more likely to be found in sagebrush islands. They generated 40 random points within the potential habitat map using Hawth's ArcGIS analysis tools (Beyer 2004) and chose another 40 non-random points in the field. The authors surveyed for pygmy rabbit sign (burrows, pellets, visual id), collected vegetation and soil characteristics, and placed an infrared camera at each sample site. Mean sagebrush cover (47%) was positively correlated with occupied sites, whereas sagebrush height was not an important factor compared to other variables. Pygmy rabbits were more likely to occupy sites with sagebrush islands. Larrucea and Brussard suggest these islands result from deeper and better-watered soils. Cheatgrass presence was negatively associated with pygmy rabbit presence. The authors suggest that focusing on sagebrush islands is 3.4 times more effective for locating pygmy rabbits than only general habitat mapping. They also suggested that general GIS models with random surveys are more appropriate for more mobile animals that select at larger spatial scales than that of pygmy rabbits.

Larrucea, E.S., and Brussard, P.F. 2008. Shift in location of pygmy rabbit (*Brachylagus idahoensis*) habitat in response to changing environments: Journal of Arid Environments, v. 72, no. 9, p. 1636–1643. DOI: https://doi.org/10.1016/j.jaridenv.2008.04.002

The authors assessed historic pygmy rabbit sites in Nevada and California to determine whether climate and land-use changes have influenced species distribution. They visited 105 historic sites, surveyed for pygmy rabbit signs (pellets, burrows, or visual detection), and placed infrared-triggered cameras at each site for one week. Each site was also evaluated for agricultural conversion, fire, livestock grazing, urbanization, and the presence of pinyon-juniper. Statistical analyses were used to compare mean elevation between historic extant and extirpated sites, the effect of elevation on the probability of pygmy rabbit persistence, and percent difference between historic extant and extirpated sites by land ownership and land use. Pygmy rabbits were present at 36% of historic sites. Occupied locations tended to be higher in elevation than unoccupied sites, with local extinction more likely at lower sites. Pinyon-juniper presence appeared to be negatively correlated with pygmy rabbit presence, with only one active site found at the 14% of sites with conifer encroachment. Livestock grazing was evident at 83% of sites; however, pygmy rabbits were still present at 33% of these sites. The authors suggest that climate change is driving altitudinal pygmy rabbit habitat shifts by increasing encroachment of conifers at higher elevation sites and increasing temperatures at lower elevation sites.

Lawes, T.J., Anthony, R.G., Robinson, W.D., Forbes, J.T., and Lorton, G.A. 2012. Homing behavior and survival of pygmy rabbits after experimental translocation: Western North American Naturalist, v. 72, no. 4, 569–581. https://doi.org/10.3398/064.072.0418

The authors assessed potential barriers to dispersal and survival of pygmy rabbits after translocation to habitat fragmentation. A total of 59 pygmy rabbits were captured, radio-tagged, and translocated short distances (1-2 km) across three habitat categories (open fragmented areas, contiguous big sagebrush cover, and continuous big sagebrush cover bisected by a road) and evaluated for homing behavior and survival. They recorded individual behavior, vegetation, and coordinates of capture and release sites, calculated landscape features, and then modeled survival. Of the 59 pygmy rabbits, 15 % homed back to their original capture site, 11 % successful homed across contiguous sagebrush habitat, 32 % through patchy habitat, and 5 % through sagebrush bisected by a road. Of predation-related deaths, 78 % occurred in the road-bisected habitat. Propensity to home and big sagebrush patch proximity positively impacted survival, while proximity to roads negatively impacted survival.

Lawes, T.J., Anthony, R.G., Robinson, W.D., Forbes, J.T., and Lorton, G.A. 2013. Movements and settlement site selection of pygmy rabbits after experimental translocation: The Journal of Wildlife Management, v. 77, no. 6, 1170–1181.

https://doi.org/10.1002/jwmg.572

Lawes et al. (2013) evaluated the movements and site selection of translocated pygmy rabbits in southeastern Oregon from June to December 2008. A total of 59 pygmy rabbits were captured, radio-tagged, and translocated short distances (1-2 km) across three habitat categories (open fragmented areas, contiguous big sagebrush cover, and continuous big sagebrush cover bisected by a road). Individuals' post-release movements and settlement site selection were tracked and analyzed using spatial analysis software and GIS. Pygmy rabbits, on average, settled on sites that had greater sagebrush cover, landscape connectivity, and fewer but larger patches of big sagebrush than those compared to their original capture sites. The current or past presence of pygmy rabbits also influenced site selection; all translocated rabbits in this study settled in areas with either active or inactive burrows. Settlement distances observed after translocation (0.02-3.5 km) were within ranges reported in other studies on the dispersal of juvenile pygmy rabbits (0.02-11.9km, Estes-Zumpf and Rachlow 2009).

Lenard, S., P. Hendricks, C. Currier, and B. A. Maxell. 2005. Pygmy rabbit distribution in Beaverhead and Madison Counties. A report to the Bureau of Land Management, Dillon Field Office. Montana Natural Heritage Program, Helena, MT. 21 pp. plus appendices. https://archive.org/details/2261F449-2D51-4200-A18F-56FFF206C7E6

Using a GIS model, the Montana Natural Heritage Program predicted pygmy rabbit distribution in Beaverhead and Madison Counties. Researchers conducted field surveys in 2004 and 2005 in areas of historic pygmy rabbit use and areas of potential habitat. Occupancy data was then paired with elevation, slope, depth to bedrock, clay content, and vegetation cover types to develop four predictive maps of pygmy rabbit habitat. Researchers trained and validated the GIS model using pygmy rabbit occupancy data. The resulting models were separated into conservative and liberal categories. Variables used in the conservative models generally fit 70% of pygmy rabbit locations, whereas variables in the liberal approach fit 90% of the locations or more. The conservative models explained 50% of the known pygmy rabbit locations, while the liberal models explained 93% of the location. Neither model was field validated, and vegetation cover classes were recognized as a limiting factor in model accuracy. The vegetation cover class layer was at a resolution of 30-m. However, misidentified pixels or pixels assigned to the dominant vegetation appeared to be poor predictors of sagebrush cover. Pygmy rabbits are patchily distributed on the landscape, often selecting for sagebrush islands. These islands may be mapped as a vegetation type other than sagebrush in raster datasets. Lenard et al. (2005) suggested that pygmy rabbits may select burrow locations at a much finer scale than what can be predicted by a GIS model.

Lyman, R.L. 1991. Late Quaternary biogeography of the pygmy rabbit (*Brachylagus idahoensis*) in eastern Washington: Journal of Mammalogy, v. 72, no. 1, 110–117. https://doi.org/10.2307/1381985

Pygmy rabbits in the Columbia Basin of eastern Washington are disjunct from Great Basin populations. The author sought to review available archeological data that may indicate that this disjunction occurred during the latest Pleistocene and earliest Holocene. Lyman examined animal remains from 189 archeological sites from the Holocene across eastern Washington and found six sites with pygmy rabbit remains. The author identified one record at a mid-Holocene site; the other five at late-Holocene sits, of which one record was within the historic Pleistocene range. No records indicate the species existed beyond the current north or south of the current eastern range during the Holocene. The late Holocene records contained fewer pygmy rabbit remains than observed in earlier periods. Lyman suggests the reduction in pygmy rabbit remains in the late Holocene indicates a reduction in pygmy rabbits in eastern Washington within the last 3,000 years. Furthermore, the findings suggest that areas to the north, west, and east of the current population were likely to support sagebrush and, therefore, pygmy rabbit populations. The author states that the current reduction in range and relative abundance in easter Washington is a continuation of a pattern that started in the late Holocene, approximately 4,000 years ago.

Lyman, R.L. 2004. Biogeographic and conservation implications of late Quaternary pygmy rabbits (*Brachylagus idahoensis*) in eastern Washington: Western North American Naturalist, v. 64, no. 1, p. 1–6. https://jstor.org/stable/41717335

The author refined a biogeographical model originally published in 1991 with eleven new pygmy rabbit historical records. Lyman suggests that these new records indicate that the pygmy rabbit had not reached its maximum range at the end of the Pleistocene. Rather pygmy rabbits had begun colonization of eastern Washington during this time. The author stated that the current disjunction between the Columbia Basin and Great Basin populations likely existed during the late Holocene. Furthermore, Lyman suggests that the prehistoric range of pygmy rabbits may have been larger than previously documented and hypothesizes that the species existed in areas not yet found.

McMahon, L.A., Rachlow, J.L., Shipley, L.A., Forbey, J.S., and Johnson, T.R. 2017. Habitat selection differs across hierarchical behaviors: selection of patches and intensity of patch use: Ecosphere, v. 8, no. 11, article e01993, 14 p. https://doi.org/10.1002/ecs2.1993

The authors examined pygmy habitat selection at two behavioral levels: broad-scale patch selection and fine-scale intensity of patch use. They collared 42 pygmy rabbits over two years and measured habitat characteristics in and near 288 winter habitat patches and 170 summer habitat patches. They measured used and unused available habitats within each rabbit's core area, made estimates of concealment, and counted entrance burrows within each habitat patch. The authors used a two-stage hurdle model to quantify initial selection and intensity of use of available resources. During winter and summer, pygmy rabbit initial patch selection was most influenced by security resources (presence and proximity of burrows, shrub height, and wood ground cover). Forage availability influenced intensity of patch use, which differed seasonally. Pygmy rabbits selected patches with greater sagebrush canopy during the winter when sagebrush is their primary forage, whereas patches with greater herbaceous forage were more intensively used during summer when pygmy rabbits' diet is varied.

Montana Natural Heritage Program (MNHP). 2016. Pygmy rabbit (*Brachylagus idahoensis*) predicted suitable habitat models created on September 10, 2016. Montana Natural Heritage Program, Helena, MT. 15 pp. http://mtnhp.org/models/files/Pygmy_Rabbit_AMAEB04010_20160910.pdf.

The Montana Natural Heritage Program (MNHP) developed an inductive and deductive model for pygmy rabbits in Montana. The goal of the inductive model was to predict the distribution and relative suitability of pygmy rabbit habitat across the species' known range within Montana using presence-only data from the MNHP database. The inductive model was created at a large spatial scale and based on abiotic and biotic layers at various scales using Maxent. The variability in spatial resolution of layers and spatial accuracy of training and testing data were limiting factors in the inductive model. The inductive model appeared to be indicative of the species' known range but should not be utilized for areas less than 64 hectares (one-quarter of a public land survey system section). The inductive model output was reclassified into suitability classes based on defined thresholds.

The goal of the deductive model was to model habitat associations closely or occasionally associated with pygmy rabbits year-round. Burkholder (2016) used statewide landcover classifications at 30x30 meter raster pixels. Constraints of landcover data limit the deductive model. Pygmy rabbits are patchily distributed, and caution should be used when using landcover associations in assessing small, patchy areas of habitat. For instance, a 30-m pixel may be incorrectly classified based on intersecting landcover types. Using presence-only data, the deductive model was evaluated using known pygmy rabbit distributions and absolute validation indices (Hirzel et al. 2006). The authors classified model outputs into commonly-, occasionally- and not-associated categories.

Olsoy, P.J., Shipley, L.A., Rachlow, J.L., Forbey, J.S., Glenn, N.F., Burgess, M.A., and Thornton, D.H. 2018. Unmanned aerial systems measure structural habitat features for wildlife across multiple scales: Methods in Ecology and Evolution, v. 9, no. 3, p. 594–604. https://doi.org/10.1111/2041-210X.12919

The authors' goal was to test unmanned aerial systems (UAS) for evaluating broad and fine-scale habitat quality indicators of pygmy rabbits. They compared UAS-derived estimates of vegetation height, volume, and canopy cover to terrestrial laser scanning (TLS, ground-based measurement) and field-based measurements. Then they mapped habitat features in two areas of Idaho using point clouds derived from UAS. UAS and TLS estimates were similar for individual plant height, volume, and canopy cover, whereas field-based measurements differed. However, UAS measurements fit field-based measurements at the patch scale better. The authors suggest that errors in field-data collection may explain the differences at the individual plant scale. Furthermore, they suggest that UAS estimates can accurately estimate habitat heterogeneity at multiple scales for vertebrate species like the pygmy rabbit.

Parsons, M.A., Barkley, T.C., Rachlow, J.L., Johnson-Maynard, J.L., Johnson, T.R., Milling, C.R., Hammel, J.E., and Leslie, I. 2016. Cumulative effects of an herbivorous ecosystem engineer in a heterogeneous landscape: Ecosphere, v. 7, no. 3, article e01334, 17 p. https://doi.org/10.1002/ecs2.1334

The authors quantified the direct and indirect effects of pygmy rabbits on soil and vegetation surrounding their burrows and evaluated whether cumulative effects resulted from pygmy rabbit occupancy. They collected habitat and soil characteristics on occupied and unoccupied mima mounds for one to twelve years in Lemhi Valley of Idaho. The spatial influence of pygmy rabbit burrowing impacted soil properties and increased nitrogen levels at the burrow entrance. Whereas the vegetation on occupied mima mounds was reduced over time through pygmy rabbit browsing. However, sagebrush reproduction over time was positively correlated with burrow occupancy, suggesting that pygmy rabbit occupancy may positively influence sagebrush reproduction and recruitment.

Pierce, J.E., Larsen, R.T., Flinders, J.T., and Whiting, J.C. 2011. Fragmentation of sagebrush communities—Does an increase in habitat edge impact pygmy rabbits? Animal Conservation, v. 14, no. 3, p. 314–321. https://doi.org/10.1111/j.1469-1795.2010.00430.x

The authors sought to understand the effects of edge habitat and fragmentation of sagebrush communities on pygmy rabbits. Sagebrush removal treatments were conducted in southern Utah to improve herbaceous understory growth in pygmy rabbit habitat. Land managers designed sagebrush removal treatments to leave habitat corridors for multiple species in drainages. The authors used these treatments to evaluate the effects of edge on pygmy rabbits by quantifying the number of active burrows relative to the edge habitat. Camera traps were placed at burrows various distances from edge habitat, and fecal pellets were counted to document species present, including competitors and predators. The authors found that the proportion of active burrows decreased within 100 m or less of edge, and that there was an increase of potential competitors (cottontails and jackrabbits) and predators near edge habitat. The reduction of burrows and relative abundance of pygmy rabbits near edge habitat was associated with an increase in predators and competitors.

Rachlow, J. L., and L. K. Svancara. 2006. Prioritizing habitat for surveys of an uncommon mammal: A modeling approach applied to pygmy rabbits. Journal of Mammalogy 87:827-833. https://doi.org/10.1644/05-MAMM-A-387R2.1

Rachlow and Svancara (2006) developed a habitat model using broadscale spatial analysis to prioritize habitat for surveys for the pygmy rabbit in Idaho. A base map of potential habitat was defined using vegetation and soil depth. The authors overlaid pygmy rabbit occurrence data with vegetation type, elevation, slope, average percent clay in the soil, and fire history. Values that encompassed >80% of all known occurrences were considered high priority and received a value of 1. Values outside that range were a lower priority and were assigned a rating of 2. Priority values (1 or 2) were averaged for each 30 m^2 of potential habitat by overlaying the GIS layers. The model's field validation occurred through random sampling of sites stratified by priority rank; surveyors also sampled sites outside of predicted habitat. Field measurements included slope, elevation, veg type, soil depth, and evidence of recent fires at each randomly selected site. Additionally, equal effort surveys were used to determine pygmy rabbit presence or absence. The model was evaluated model by determining how well habitat variables on the ground were classified correctly into high or lower priority categories for each habitat variable. Overall model accuracy was 65% when presence-absence was evaluated against the two highest and two lowest predictive habitat categories using Cohen's kappa statistic. Vegetation type and fire history were the most informative characteristics in predicting habitat. Rachlow and Svancara (2006) made the distinction between potential habitat versus unoccupied habitat. Unoccupied sites in mapped potential habitat areas may become occupied in the future, which is relevant when making land management decisions. They also cautioned that coarse grain soil depth and vegetation layers are likely limiting factors in building predictive habitat maps for pygmy rabbits.

Sanchez, D.M., and Rachlow, J.L. 2008. Spatio temporal factors shaping diurnal space use by pygmy rabbits: Journal of Wildlife Management, v. 72, no. 6, p. 1304–1310. https://doi.org/10.2193/2007-225

Sanchez and Rachlow sought to evaluate variation between sexes in movement and home range size, whether there were seasonal differences in space use, and how site-specific habitat resources influenced space use patterns. The researchers trapped and collared pygmy rabbits in east-central Idaho between 2004 and 2005 at three sites that differed in food distribution and cover resources. They maintained a sample size of 36 to 48 radio-collared rabbits throughout the study. Annual and seasonal home rangers were estimated, and the authors evaluated the number and spatial arrangement of burrow systems between seasonal and annual periods. The authors also examined whether individuals shifted their home ranges between seasons and years. They found that pygmy rabbit space use was influenced by both sex and season. Male rabbits had larger home ranges and core areas, larger burrow systems, and more widely dispersed burrow systems than females. The home range size of male rabbits increased by about 300% during the breeding season, whereas female home ranges remained stable across seasons. Seasonal home ranges varied across study sites, suggesting that the distribution of habitat resources influenced the space use of individual rabbits. Pygmy rabbits at sites with higher sagebrush cover had larger home ranges than those at sites with lower and clumped cover resources. The authors suggest that pygmy rabbits have larger home ranges than predicted by allometric models due to the high energy demands of the species. The authors point out that the differences between home range size estimates between sexes being substantially larger than those reported by Burak (2006) likely reflects differences in space use and resources between study sites. Finally, Sanchez and Rachlow (2008) recommend that wildlife managers consider larger areas of habitat among seasons for pygmy rabbits and site-scale resource characteristics when considering management actions.

Schmalz, J.M., Wachocki, B., Wright, M., Zeveloff, S.I., and Skopec, M.M. 2014. Habitat selection by the pygmy rabbit (*Brachylagus idahoensis*) in northeastern Utah: Western North American Naturalist, v. 74, no. 4, p. 456–466. https://doi.org/10.3398/064.074.0411

The authors sought to examine the occurrence, habitat selection, and diet of pygmy rabbits in northeastern Utah to evaluate burrow and food selection. They conducted pygmy rabbit surveys along nine transects in the spring and summer of 2010 and categorized burrows as active, recently active, old, very old, or excavated based on established criteria. The researchers also surveyed and classified burrows as active or recently active through the presence of fresh, recent, or old pellets (Sanchez et al. 2009). They collected vegetation and soil measurements at occupied and unoccupied sites. In December, they took foraged and non-foraged sagebrush samples to conduct a nutrient analysis. Schmalz et al. (2014) found that sagebrush at burrow sites was taller, had larger crown widths, and provided more cover than potential burrow sites ($P < 0.001$).

However, there was no difference in density to the nearest sagebrush or number of sagebrush within a 3-m radius between burrows and potential burrows. Total forb and grass biomass were higher at active burrows in the spring than at potential and abandoned sites ($P < 0.005$). Pygmy rabbit's annual diet at the study site consisted of 80.7% sagebrush and foraged sagebrush was higher in crude protein and lower in fiber than non-foraged sagebrush

Simons, E. M., and J. W. Laundre. 2004. A large-scale regional assessment of suitable habitat for pygmy rabbits in southwestern Idaho. Northwest Science 78:33-41.

Simons and Laundre (2004) adapted a previous pygmy rabbit GIS model from the Idaho National Engineering Lab (INEL) (Gabler and Laundre 2000) to the southwestern corner of Idaho. They used GAP vegetation data (30 m), STATSGO soils data (80 m), and derived slope, aspect, and elevation from a USGS digital elevation model (30 m) for the study area. Due to soil data, the final habitat suitability map was at a resolution of 80 m. The overall accuracy of the model at predicting suitable habitat was 79%, and the accuracy of the vegetation layer was 77%. The model predicted that 21% of the study area was suitable pygmy rabbit habitat. However, suitability was indicative of pygmy rabbit presence rather than potential habitat. The model did not perform well at predicting use areas, potentially due to the low density of pygmy rabbits within the study area. The authors also recognized that other variables not included in the model might be important when predicting pygmy rabbit distributions. For example, the density of grasses and forbs (Heady 1998) may be important at finer scales than what can be captured when conducting a coarse-scale analysis. Simons and Laundre (2004) suggested the model may do a better job of predicting non-use areas due to the degree of patchiness of the species, whereas there is more site scale variation observed in areas of potential habitat.

Smith, I.T., Rachlow, J.L., Svancara, L.K., McMahon, L.A., and Knetter, S.J. 2019. Habitat specialists as conservation umbrellas—Do areas managed for greater sage grouse also protect pygmy rabbits?: Ecosphere, v. 10, no. 8, article e02827, 23 p. https://doi.org/10.1002/ecs2.2827

Smith et al. (2019) assert that designated habitat management areas for sage-grouse act as a conservation umbrella for pygmy rabbits. Using maximum entropy methods, the authors developed a range-wide species distribution model with presence-only records. The authors reviewed and thinned 10,420 pygmy rabbit records across the species range. They selected environmental variables based on published research (topography, soils, vegetation, climate, and fire regime) and associated spatial layers. These spatial layers and occupancy data were then projected into a common coordinate system (NAD 1983 Albers) and resampled to 30-m. Using the program Maxent (Maxent 3.4.0, Phillips et al. 2016), Smith et al. created a species distribution habitat model using the thinned occurrence data and environmental variables. The resulting output measures the degree of similarity to known sites and is represented in a grid cell by a value between 0 and 1. The model was trained using 80% of the occurrence records, and the remaining 20% were used for model validation. The resulting range-wide pygmy rabbit species distribution map was then classified into three habitat classes (primary, suitable, unsuitable) using two threshold values. Smith et al. estimated 92% of the entire pygmy rabbit population's minimum occupied area, and 87% of modeled suitable habitat falls within designated sage-grouse habitat management areas, where habitat and surface disturbance is limited, and focused efforts are made to improve habitat. Smith et al. suggest finer-scale analyses on pygmy rabbit movement and dispersal are needed to further evaluate patterns of habitat overlap between sage-grouse and pygmy rabbit.

Smith, I. T., Knetter, S. J., Svancara, L. K., Karl, J. W., Johnson, T. R., and Rachlow, J. 2021. Overlap between sagebrush habitat specialists differs among seasons: Implications for umbrella species conservation. Rangeland Ecology & Management. 78. 142-154. https://doi.org/10.1016/j.rama.2021.06.007

The authors sought to evaluate the degree to which greater sage-grouse seasonal habitats overlap with the pygmy rabbit in east-central Idaho. The greater sage-grouse is considered an umbrella species for sagebrush ecosystems due to its range of habitats used across seasons. In contrast, the pygmy rabbit is patchily distributed with specific habitat requirements at finer scales. To compare habitat overlap, the authors developed inductive species distribution models (SDMs) using maximum entropy for greater sage-grouse and pygmy rabbits. They developed four SDMs for sage-grouse, including three seasonal models (spring, late brood-rearing, and winter), one general distribution model, and a single SDM for pygmy rabbits. The authors used land cover, topography, and phenology as environmental covariates for both species and bioclimatic variables and soil properties for the pygmy rabbit SDM. The spatial resolution of all variables was 90-m. However, the authors characterized conditions at multiple spatial scales (fine, mid, broad-scale) using focal statistics and various-size neighborhoods based on sage-grouse movements and ecology. The resulting models showed that potential sage-grouse distribution encompassed 73% of all suitable pygmy rabbit habitat within the study area. However, this proportion dropped to 49% when considering highly suitable habitat only. Highly suitable sage-grouse habitat tended to occur at lower elevations and was more widely distributed than highly suitable pygmy rabbit habitat. Additionally, habitat overlap varied seasonally between 42-65% for suitable habitat, and 18-31% overlap for highly suitable habitat. The authors assert that habitat conservation for pygmy rabbits is needed in areas that do not overlap with seasonal protections conferred through policy actions for the sage-grouse. Further, they suggest incorporating spatial and temporal scales when considering the effectiveness of conservation strategies for umbrella species.

Thines, N.J.S., Shipley, L.A., and Sayler, R.D. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*): Biological Conservation, v. 119, p. 525–534. https://doi.org/10.1016/j.biocon.2004.01.014

The authors sought to understand the effects of cattle grazing on burrow distribution, habitat components, forage quality, and diet of the endangered Columbia Basin pygmy rabbit. They compared the effects of four grazing treatments on the distribution of pygmy rabbits in Sagebrush Flat study area in 2000. The researchers located burrows and recorded activity between July and September to assess burrow use. Fecal pellets were collected and dissected between August and December to assess diet. Vegetation was sampled in June, December, and March of 2000 to determine crude protein and fiber. The authors measured vegetation characteristics in grazed and ungrazed plots between 1996 and 2000. Spatial analysis showed grazed and ungrazed areas differed in soil types and indicated pygmy rabbits used southwest aspects disproportionate to availability. The authors found that ungrazed areas had a higher density of burrows than grazed plots. Vegetation composition and structure did not differ significantly at plots in the early spring prior to grazing. However, late summer through winter grazing reduced the nutritional quality of grass for pygmy rabbits and reduced herbaceous cover by 50%. The authors suggested that the reduction of grasses and forbs may be detrimental to the summer diet of pygmy rabbits in grazed areas. Furthermore, pygmy rabbits appeared to prefer areas ungrazed by cattle, and removing cattle from areas important to pygmy rabbit conservation may be beneficial.

Wilson, T.L., Odei, J.B., Hooten, M.B., and Edwards, T.C., Jr. 2010. Hierarchical spatial models for predicting pygmy rabbit distribution and relative abundance: Journal of Applied Ecology, v. 47, p. 401–409. https://doi.org/10.1111/j.1365-2664.2009.01766.x

The author's goal was to develop a hierarchical spatial model to predict pygmy rabbit distribution and relative abundance using two indirect measures of presence. They suggest that the inclusion of hierarchically related indirect detection data (burrow counts and fecal pellets) as model inputs incorporates measures of spatial structure and uncertainty. Assessing spatial structure and measures of uncertainty can be problematic in species distribution models for rare or cryptic species. The authors conducted distance sampling at 38 sites in Rich County, Utah. They counted burrows along transects and documented the presence or absence of fecal pellets at burrow entrances. They used a hierarchical Bayesian framework to model burrow intensity and probability of utilization along with spatial covariates (slope, aspect, distance to water, and vegetation characteristics). The resulting maps of burrow intensity and utilization predicted higher burrow abundance on slopes near drainages, in valleys of the study area, and lower abundance in agriculture fields. Burrow intensity was positively associated with northing, slope, and soil moisture, and high burrow utilization was positively associated with soil and snow deposition and red band reflectance (a visual signature of sagebrush). Both burrow intensity and utilization were negatively related to easting, near-infrared reflectance (a visual signature of agricultural fields), and distance to water. The authors suggest that previous predictive pygmy rabbit models that used untransformed aspect values showed inconsistent results due to confounding variables rather than differences between study areas. The authors further suggest that future models that incorporate indirect measures of presence will be more accurate, especially for modeling the distribution and abundance of cryptic species.

Wilson, T.L., Howe, F.P., and Edwards, T.C., Jr. 2011. Effects of sagebrush treatments on multi-scale resource selection by pygmy rabbits: Journal of Wildlife Management, v. 75, no. 2, p. 393–398. https://doi.org/10.1002/jwmg.51

Removal of sagebrush has been used to improve forage for livestock and big game through the release of the herbaceous understory. However, such treatments may negatively affect sagebrush obligate species like the pygmy rabbit. The authors evaluated the effects of sagebrush removal on second and third-order habitat selection of pygmy rabbits in Woodruff, Utah. They also evaluated pygmy rabbit behavior at treatment edges. They radio-collared eight pygmy rabbits in the spring of 2008 and tracked them for one year. Weekly telemetry locations were used to estimate home ranges for each rabbit and daily snow tracking in the winter was used to evaluate behavior near treatment edges. The estimated home ranges and telemetry point locations were evaluated for avoidance behavior of treated areas using null models at second and third order habitat selection scales (Johnson 1980). Pygmy rabbit home range location did not appear to be impacted by sagebrush removal treatments. However, the two rabbits that occurred closest to the treatment areas appeared to avoid the treatments compared to random null locations, suggesting within home range selection against the treatments. The winter track surveys also supported these findings.

Woods, B.A., Rachlow, J.L., Bunting, S.C., Johnson, T.R., and Bocking, K. 2013. Managing high-elevation sagebrush steppe—Do conifer encroachment and prescribed fire affect habitat for pygmy rabbits?: Rangeland Ecology and Management, v. 66, no. 4, p. 462–471. https://doi.org/10.2111/REM-D-12-00144.1

Changes in fire regimes in sagebrush steppe habitat have caused conifer encroachment at higher elevations. The subsequent increase in conifer cover in sagebrush habitat may have a detrimental effect on sagebrush obligate species, like the pygmy rabbit. The authors evaluated how increasing conifer cover and prescribed burning may affect pygmy rabbit forage availability and predator detection and avoidance. They established five plots in each of the ten historic prescribed burns within the study area. One plot was inside the burn perimeter, three plots within denser conifer cover, and one plot in a reference sagebrush site with no conifer cover. The ten burns ranged from 6 to 32 years post-fire. They assessed vegetation cover, composition, and biomass, analyzed fecal pellets, and quantified concealment and visibility from terrestrial and aerial predators at each plot. Sites with higher conifer cover provided less concealment from terrestrial predators and had reduced forage availability. Sites that had been burned more recently had less sagebrush cover, while grass cover was higher. Sites that had been burned took between 13 to 27 years to resemble reference sagebrush sites. Woods et al. (2013) suggest that prescribed burns to reduce conifer cover will also reduce sagebrush cover and make sites unsuitable for pygmy rabbits.

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APPENDIX A. TABLES

Table 1. Summary of pygmy rabbit habitat models by year, study area, model type, environmental variables modeled, and the model accuracy or specificity if evaluated. All models included landcover type and soil properties as environmental variables, and all models excepting Meisel (2006) used topography. Percent accuracy or specificity was assessed in the majority of models; however, these values are not comparable between models due to differences in model type and methodology used.

Author	Gabler and Laundre (2000)	Heady et al. (2001)	TNC (2004)	Simons and Laundre (2004)	WY Natural Diversity Database (2004)	Lenard et al. (2005)	MT NHP (2006)	Rachlow and Svancara (2006)
Study Area	INEEL ID	INEEL ID	SW WY	SW ID	SW WY	Beaverhead and Madison Counties, MT	MT	ID
Model Type	Predictive habitat map	Predictive habitat map	SDM and range map	Predictive habitat map	SDM and range map	Predictive habitat map	SDM	Predictive habitat map
Landcover	x	x	x	x	x	x	x	x
Soil Properties	x	x	x	x	x	x	x	x
Topography	x	x	x	x	x	x	x	x
Climate					x			
Phenology								
Fire history								x
Development								
Model accuracy or specificity in predicting potential habitat or occupancy	The model was successful in predicting areas not occupied (100% accurate) and 57% occupied.	Accuracy of predicting pygmy rabbit use areas was 57% probability.	73.9% occupied 50.6% unoccupied	Overall accuracy of predicting suitable habitat (79%)	67% occupied 55.8% unoccupied	Conservative models explained 50% of pygmy rabbit occurrences, Liberal models explained 93%	Average Testing Deviance ($\bar{x} \pm$ sd) = 1.625 ± 1.301 Training AUC = 0.881 Test AUC = 0.855	65% overall model accuracy

Table 1 continued.

Author	Miesel (2006)	Hagar and Lienkaemper (2007)	Himes and Drohan 2007	Larrucea and Brussard 2008	Carr and Melcher. (2017)	Smith et al. (2019)	Smith et al. (2021)	Rush (2021)
Study Area	Hartford NWR	Oregon	NV	CA/NV	Wyoming Basin	Range wide	Idaho	5 Regional SDMs for ID
Model Type	Predictive habitat map	Predictive habitat map	Predictive habitat map	Predictive habitat map	SDM	SDM	SDM	SDM
Landcover	x	x	x	x	x	x	x	x
Soil Properties	x	x	x	x	x	x	x	x
Topography		x	x	x	x	x	x	x
Climate					x	x	x	x
Fire history						x		
Phenology							x	x
Development					x			
Model accuracy or specificity in predicting potential habitat or occupancy	Not evaluated	Not evaluated	The model explained 56.7% positive occurrence	79% occupied	Not evaluated	Maximum test sensitivity plus specificity threshold of 0.3167 for range-wide suitable habitat	AUC of 0.854	Region 1- AUC 0.030 Region 2- AUC 0.927 Region 3- AUC 0.861 Region 4 – AUC 0.936 Region 5 - AUC 0.821

Table 2. Broad management topics were assigned to each article/report after an initial structured literature search (Carter 2019, Carter 2020, Kleist 20201). Definitions of each broad management category are provided. Peer-reviewed papers that I assigned one of the categories: biogeography, habitat characteristics (site and/or broad scale), dispersal, habitat characteristics, and distribution models were then refined further under hierarchal habitat selection.

Category	Description
Animal behavior	Study measured or modeled aspects of species behavior or demographics (for example, seasonal movements, reproductive success, vital rates).
Biogeography	Study addressed distribution of pygmy rabbits and habitat geographically and throughout geological time and space.
Captive breeding	Study addressed off-site conservation techniques used to supplement wild populations of pygmy rabbits. Study developed methods for or evaluated the success of captive breeding efforts.
Capture or survey techniques	Study developed methods or evaluated efforts of specific survey or capture techniques.
Conifer expansion	Study addressed effects of conifer expansion or conifer removal treatments on species habitat, populations, or individuals.
Diet	Study addressed pygmy rabbit nutritional requirements and food selection.
Disease ecology	Study addressed parasites, pathogens, or infectious diseases found in pygmy rabbit populations or individuals.
Dispersal	Study addressed physical movement of pygmy rabbits between a source location (e.g., natal site) to another location where establishment or reproduction may occur.
Energy Development (Oil and Gas)	Study addressed effects of energy development on species habitat, populations, or individuals.

Category	Description
Genetics	Study used genetic evidence to investigate species biology (for example, population structure, connectivity, behavior).
Grazing	Study addressed effects of herbivory (wild or domestic) on species habitat, populations, or individuals.
Habitat characteristics (site scale)	Study addressed habitat characteristics at the local level (for example, burrows), typically based on field measurement of vegetation or soils.
Habitat characteristics (broad scale)	Study addressed landscape-level habitat characteristics (for example, size, number, or connectivity of habitat patches; characteristics of linkage areas; effects of landscape context on habitat quality; availability or use of habitats), usually across large areas.
Habitat connectivity	Study addressed the degree to which habitat patches are connected, and how pygmy rabbits move between patches.
Habitat restoration	Study addressed methods for habitat restoration or the responses of the species or their habitat to restoration efforts.
Invasive plants	Study addressed effects of nonnative invasive plant species (or efforts to control those species) on the species or their habitat
Physiology	Study focused on pygmy rabbit biological functions, such as regulation of temperature, blood flow, or hormones.
Population estimates	Study estimated or modeled species population numbers, trends, dynamics, assessment methods, or responses to the environment.
Sagebrush removal	Study addressed effects of intentional sagebrush removal treatments on species habitat, populations, or individuals.

Category	Description
Species accounts and natural history	Study describes survey results and observational data.
Species and habitat distribution models	Study developed and evaluated a species or habitat distribution model.
Translocations	Study developed methods for or evaluated the success of species translocation efforts.

Table 3. Habitat selection scales were assigned to each article for consideration. Papers focused on first through third order habitat selection (Johnson 1980) were included in the bibliography.

Habitat selection scale	Defined
First-order	The selection of the physical or geographical range of a species.
Second-order	The home range of an individual or social group within their geographical range.
Third-order	How habitat components within the home range are used (i.e., areas used for foraging or burrowing)
Fourth-order	How components of a habitat are used (i.e., if third-order selection determines a foraging patch, fourth-order selection would be the actual selection of individual food items at that site).
Multiple scales	The study focused on multiple habitat selection scales.

Table 4. Potential environmental variables (land cover, topography, phenology, climate, soil properties, and disturbance history) that could be used to model pygmy rabbit habitat or distribution are reported. Relevant research and potential thresholds for each variable are described.

Type	Environmental variable	Notes/supporting research
Land cover	Mean sagebrush cover (%) Mean sagebrush height (cm)	• Sagebrush patches with higher obscurity provide concealment from predators (Camp et al. 2012). • Sagebrush makes up between 80-99% of the winter diet of sagebrush and approximately half of their summer diet (Green and Flinders 1980, Shipley et al. 2006). • Sagebrush provides security and thermal cover (Milling et al. 2017). • Percent understory composed of shrubs and sagebrush and percent decadence of sagebrush were found to be important variables influencing site scale selection of pygmy rabbits in Utah (Edgel et al. 2014). Shrub cover appears to be an important variable in site selection in California, Idaho (Gabler et al. 2001, Heady et al. 2001), Nevada, Oregon (Hagar and Lienkaemper 2007), and Wyoming (Green and Flinders 1980, Weiss and Verts 1984, Katzner and Parker 1997, Larrucea and Brussard 2008).
	Perennial grass cover (%) Perennial forb cover (%)	• Grasses and forbs make up approximately half of the pygmy rabbit's diet during the summer (Shipley et al. 2009, Schmalz et al. 2014). • The herbaceous understory provides concealment during the summer months.

Type	Environmental variable	Notes/supporting research
	Herbaceous cover (%) Annual invasives cover (%)	• Pygmy rabbits prefer habitat patches with higher terrestrial cover (Crowell et al. 2016). • Pygmy rabbits selected for a higher diversity of forbs, complex vegetation profile, and high shrub cover near burrow sites on the in southern Idaho (Heady et al. 2001, Heady and Laundré 2005). • The presence of cheatgrass was negatively associated with pygmy rabbit presence (Larrucea and Brussard 2008). • Total forb and grass biomass was higher at active burrows in the spring than at potential and abandoned sites ($P < 0.005$) (Schmalz et al. 2014)
	Percent litter (%) Percent bare ground (%)	• Areas of reduced ground litter and micro biotic crusts are associated with pygmy rabbit burrows (Weiss and Vert 1984, Himes and Drohan 2007, Edgel et al. 2014).
	Tree canopy cover (%) Proportion of landscape with >3% canopy cover	• Tree cover provides perches for avian predators. • Increasing tree cover is associated with a reduction in shrub understory (Larrucea and Brussard 2008, Woods et al. 2013, Edgel et al. 2014). Pinyon-juniper presence appeared to be negatively correlated with pygmy rabbit presence, with only one active site found at 14% of sites with conifer encroachment in Nevada and California (Larrucea and Brussard 2008).
	Percent agriculture (%)	• Agricultural lands are avoided by pygmy rabbits. Agricultural development may increase isolation and inhibit gene flow between pygmy rabbit populations (Estes-Zumpf et al. 2014).

Type	Environmental variable	Notes/supporting research
	Proportion of landscape in agriculture	• Although some pygmy rabbits may use areas adjacent to agricultural at local scales.
Topography	Mean elevation Terrain roughness (SD of elevation) Topographic Position Index (TPI) Slope position General landforms Aspect	• Pygmy rabbits in Utah and Nevada occurred at higher elevations (Edgel et al. 2014, Larrucea and Brussard 2008). • Survey sites where pygmy rabbits were present were closer to perennial streams, had greater soil depth, and had more northerly aspects relative to areas where pygmy rabbits were not observed (Himes and Drohan 2007). • Burrow intensity was positively associated with northing, slope, and soil moisture, and high burrow utilization was positively associated to soil and snow deposition, as well as red band reflectance (a visual signature of sagebrush) (Wilson et al. 2010).
Phenology	Vegetation productivity (mean NDVI during summer months, average of monthly maximums), (intra-seasonal average and	• Vegetation productivity was shown to influence pygmy rabbit distribution in Idaho with a relative variable importance (percent contribution/permutation importance) of 12.8/10.5(Smith et al. 2021). • Pygmy rabbits selected patches with greater sagebrush canopy during the winter when sagebrush is their primary forage, whereas patches with greater herbaceous forage were more intensively used during summer when pygmy rabbit's diet is varied (McMahon et al. 2017).

Type	Environmental variable	Notes/supporting research
	standard deviation of monthly maximums between years of interest)	• Total forb and grass biomass was higher at active burrows in the spring than at potential and abandoned sites ($P < 0.005$) (Schmalz et al. 2014). • Both burrow intensity and utilization were negatively related near infrared reflectance (a visual signature of agricultural fields) and distance to water (Wilson et al. 2010)
Climate	19 bioclimatic variables (Hijmans et al. 2005)	• Pygmy rabbits are endotherms that can be affected by seasonal thermal extremes (Katzner and Parker 1997, Milling et al. 2018) • Pygmy rabbits are a resident species and do not migrate between seasonal habitat areas, rather they utilize burrows and micro-sites as seasonal thermal refuges (Milling et al. 2018). • Larrucea and Brussard (2008) suggest climate change is driving altitudinal pygmy rabbit habitat shifts by increasing encroachment of conifers at higher elevation sites and increasing temperatures at lower elevation sites.
Soil Properties	Clay in 0-30cm & 30-100cm (%) Sand in 0-30cm & 30-100cm (%) Silt in 0-30cm & 30-100cm (%) pH in 0-30cm & 30-100cm	• Pygmy rabbits are obligate burrowers and prefer relatively deep, loamy soils (Green and Flinders 1980). • Relatively deep, well drained soils support shrub growth in areas used by pygmy rabbits (Weiss and Verts 1984). • Pygmy rabbits are often associated with microtopography such as mima mounds (Parsons et al. 2026), and areas indicative of soil deposition like drainages, alluvial fans, and hillsides (Weiss and Verts 1984).

Type	Environmental variable	Notes/supporting research
	Bulk density in 0-30cm & 30-100cm (g/cm3) Organic matter in 0-30cm & 30-100cm log10 (%) Saturated soil water content in 0-30cm & 30-100cm (m3/m3) Depth to restrictive layer (cm)	• Suitable soils have greater sand and less clay (usually less than 18%; Gabler 1997; Rachlow and Svancara 2003).
Disturbance History	Grazing history intensity	• Larrucea and Brussard (2008) • Pygmy rabbits prefer ungrazed to grazed areas. Grazing occurring during late summer and winter reduced herbaceous cover by 50% and reduced the nutritional quality of grasses for pygmy rabbits (Thines et al. 2004).
	Prescribed burn history Fire history Fire intensity	• Sites with higher conifer cover provided less concealment from terrestrial predators and had reduced forage availability. Sites that had been burned more recently had less sagebrush cover, while grass cover was higher. Sites that had been burned took between 13 to 27 years to resemble reference sagebrush sites (Woods et al. 2013).

Type	Environmental variable	Notes/supporting research
	Sagebrush removal	• Sagebrush removal resulted in a reduction of burrows and relative abundance of pygmy rabbits near edge habitat (Pierce et al. 2011). Pygmy rabbits avoided sagebrush treatments in northeastern Utah (Wilson et al. 2011).
	Oil and gas, Development, Roads (Total surface area)	• Carr et al. (2017) developed a terrestrial development index (TDI) which quantifies levels of development intensity, including agriculture, roads and railroads, and energy and minerals as total surface area for the Wyoming Basin. They found that development had effectively fragmented pygmy rabbit; only 7.8 % of relatively undeveloped areas occur in patches > 100 km^2 (Carr et al. 2017). • Energy development results in habitat loss and decreased space use by pygmy rabbits; home ranges and core areas may decrease in size due to avoidance of edge habitat created by energy development or other disturbances (Edgel et al. 2018). • Low levels of roads and streams in Idaho did not appear to inhibit pygmy rabbit dispersal (Estes-Zumpf et al. 2010). • Sharp declines in the presence and abundance of pygmy rabbits were observed after approximately 2% of the area was utilized for gas infrastructure (Germaine et al. 2017) and presence being significantly lower within 0.5-1.5 km of the nearest road and 2 km of well pads and utilities (Germaine et al. 2020). • Proximity to roads decreased survival (Lawes et al. 2012).

Table 5. Available range-wide datasets and the available resolution for environmental variables that could be used in future pygmy rabbit modeling efforts.

Type	Available Resolution	Potential Data Sources
Land cover and Productivity	30m	2019 Land Cover Database Products (Dewitz and U.S. Geological Survey 2021) 2019 Exotic Annual Grass Percent Cover (Pastick et al. 2021) Provisional Remote Sensing Shrub/Grass NLCD Base Products for the Western US (i.e., sagebrush canopy cover; USGS 2019) Rangeland Fractional Components dataset from the National Land Cover Database (Rigge et al. 2020, Rigge et al. 2021) Rangeland Analysis Platform Vegetation Cover (Allred et al. 2021)
Topography	1/3 arc-second, 10-m	USGS National Elevation Dataset (NED; USGS 2019)
Phenology	30 m	Vegetation biomass (Jones et al. 2021) Landsat Normalized Difference Vegetation Index (NDVI) (Vermote et al. 2016)
Climate	19 bioclimatic variables (Hijmans et al. 2005) - 800 m	Long-term datasets describing average conditions during 1981-2010 (PRISM Climate Group 2012)

	35 bioclimatic variables – 55 km	CMCC-BioClimInd (Noce et al. 2020)
Soil Properties	30 m	POLARIS Soil Data (Chaney et al. 2019) State Soil Geographic Data set (STATSGO) if POLARIS data is unavailable
Development	30 m	LANDFIRE EVT – Landscape Fire and Resource Management Planning, Existing Vegetation Type
Fire History	Wildlife perimeter data	National Interagency Fire Center (NIFC) – Wildland Fire Open Data

APPENDIX B. RELEVANT PRODUCTS EXCLUDED FROM THE ANNOTATED BIBLIOGRAPHY

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