PYGMY RABBIT (BRACHYLAGUS IDAHOENSIS) HABITAT SELECTION: DOES SAGEBRUSH (ARTEMISIA SPP.) AGE INFLUENCE SELECTION?

Robert J. Edgel^{1,2}, Janet L. Pierce¹, and Randy T. Larsen¹

ABSTRACT.—The pygmy rabbit ($Brachylagus\ idahoensis$) is a sagebrush ($Artemisia\ spp.$) obligate that depends on sagebrush habitats for food and cover throughout its life cycle. Invasive species, frequent fires, overgrazing, conversion of land to agriculture, energy development, and many other factors have contributed to recent declines in both quantity and quality of sagebrush habitats required by pygmy rabbits. Given declining availability of sagebrush, there is a need to identify characteristics of suitable pygmy rabbit habitat. Although habitat selection information exists from several western states, data is limited for pygmy rabbits in Utah at the extent of their range. We sampled 77 different habitat variables at occupied (n=72) and unoccupied (n=61) sites in Utah. We then used random forests to determine which variables best discriminated between occupied and unoccupied sites. We predicted that sites occupied by pygmy rabbits would have greater percentages of sagebrush, greater amounts of cover, and greater mean sagebrush age compared to unoccupied sites. Occupied sites had greater horizontal obscurity (measure of cover), occurred at higher elevations, had greater percent understory composed of sagebrush and other shrubs, and lower percent sagebrush decadence than unoccupied sites. Contrary to our predictions, sagebrush age at occupied sites was not an important variable and mean age did not differ by site type. We suggest managers use this information to help identify suitable pygmy rabbit habitats to further conservation of this imperiled lagomorph.

RESUMEN.—El conejo pigmeo (Brachylagus idahoensis) depende de la artemisas (Artemisia spp.) para alimentarse y protegerse a lo largo de su ciclo de vida. Otras especies invasoras, constantes incendios, el excesivo pastoreo, la transformación de la tierra para agricultura, el desarrollo energético y muchos otros factores han contribuido a recientes declives en ambas, en cantidad y calidad, del hábitat de artemisas necesario para los conejos pigmeos. Debido a la disponibilidad baja de artemisas, surge la necesidad de identificar las características de aquellos hábitats aptos para los conejos pigmeos. Aunque existe información de la selección de hábitat para los estados del oeste, los datos sobre los conejos pigmeos en Utah hasta el límite de su distribución, son limitados. Examinamos 77 variables de hábitats diferentes en áreas ocupadas (n = 72) y desocupadas (n = 61) en Utah. Luego, utilizamos aleatoriamente zonas forestales para identificar cuáles eran las variables que determinaban las áreas ocupadas de las desocupadas. Predijimos que las áreas ocupadas por los conejos pigmeos tendrían un mayor porcentaje de artemisas, mayor cantidad de cobertura y una edad promedio mayor de las artemisas en comparación con las áreas desocupadas. Las áreas ocupadas tenían mayor oscuridad horizontal (medida de la cobertura), se encontraban a mayor altura, presentaban un mayor porcentaje de sotobosque de artemisas y otros matorrales, y menor porcentaje de declive de artemisas que las áreas desocupadas. Contrario a nuestro pronóstico, la edad de las artemisas en las áreas ocupadas no fue una variable importante y la edad promedio no varió de acuerdo con el tipo de ubicación. Sugerimos a los responsables utilizar esta información para ayudar a identificar hábitats adecuados para el conejo pigmeo con el fin de lograr conservar a este lagomorfo en peligro.

Studies of habitat selection provide information that improves management practices by identifying areas and characteristics of preferred habitat for species of interest. The identification of such habitat characteristics is a fundamental element in the conservation and management of wildlife (Reynolds 1974). Habitat selection studies have become increasingly important as human influence continues to alter natural landscapes in ways that impact wildlife. These studies can help managers mitigate the effects of reductions in both extent and quality of remaining habitat. Habitat selection

information is particularly useful for species that are habitat obligates because these species often have greater difficulty responding to habitat changes than generalists (Larrucea and Brussard 2008c, Crow and van Riper 2010). Habitat-obligate species are also more vulnerable to degradation, fragmentation, and loss of specific ecosystem resources than are habitat generalists (Ingelfinger and Anderson 2004, Walker et al. 2007).

Pygmy rabbits (*Brachylagus idahoensis*) are small (400–500 g) lagomorphs that only occur in mature sagebrush (*Artemisia* spp.) habitats

¹Department of Plant and Wildlife Sciences and Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT 84602.

²E-mail: robertjedgel@gmail.com

(Roberts 2003, Shipley et al. 2006). Sagebrush is required by pygmy rabbits during all phases of their life cycle, and it provides both food and cover for this obligate species (White et al. 1982, Thines et al. 2004, Shipley et al. 2006). Sagebrush comprises >95% of winter and >50% of summer diet for this specialized lagomorph (Green and Flinders 1980, Thines et al. 2004). Pygmy rabbits are also semifossorial and use burrows for shelter. They are one of only 2 rabbits in North America known to excavate their own burrows and thus require soils suitable for digging in addition to sagebrush (Dobler and Dixon 1990, Sanchez et al. 2009). Soils at sites occupied by pygmy rabbits have been described as having a soft loamy texture that facilitates digging (Weiss and Verts 1984, Gabler et al. 2001).

Sagebrush habitats required by pygmy rabbits are declining in size and function throughout the western United States (Beetle 1960, Schneegas 1967, Vale 1975, Baker et al. 1976, Braun 1998, Miller 1999, Miller and Eddleman 2000, Braun et al. 2002, Bradley 2010). Factors attributed to this decline include changes in frequency and intensity of fire, invasive species, conversion of land to agriculture, overgrazing, and energy development (Barney and Frischknecht 1974, Miller 1999, Braun et al. 2002, Thines et al. 2004, Bradley 2010). Degradation of sagebrush habitats appears to be increasing because of invasive cheatgrass (Bromus tectorum) and other annual plants that have altered fire cycles (D'Antonio and Vitousek 1992, Brooks et al. 2004, Evans and Rollins 2008). These altered fire cycles negatively impact sagebrush communities and favor annual grasses unsuitable to sagebrush obligates such as pygmy rabbits. Loss and alteration of sagebrush habitats have resulted in the listing of pygmy rabbits as an endangered species in Washington State and a species of conservation concern in all other states within its geographic range (Lyman 1991, Gahr 1993, McAllister and Program 1995, USFWS 2003, Lyman 2004).

Given the ongoing loss of sagebrush habitats, it is important to identify characteristics of preferred habitat and locations of remaining suitable habitats to promote conservation of pygmy rabbits. Habitat requirements for pygmy rabbits have been described in several western states, including California (Larrucea and Brussard 2008b), Idaho (Green and Flinders 1980),

Nevada (Himes and Drohan 2007, Larrucea and Brussard 2008b), Oregon (Weiss and Verts 1984), Washington (Gahr 1993), and Wyoming (Katzner and Parker 1997). However, only limited habitat selection work has been published for pygmy rabbits in Utah, and identification of certain characteristics associated with preferred habitats (i.e., sagebrush age) is lacking (Larrucea and Brussard 2008b, Wilson et al. 2010). Moreover, the distribution of pygmy rabbits in Utah extends across much of the state and represents the southeastern extent of the species' distribution. More information on habitat selection by pygmy rabbits in Utah and closer examination of poorly understood characteristics of habitat selection such as sagebrush age will fill an information gap for this region and contribute to broader understanding of this imperiled lagomorph.

Our objective was to characterize habitat occupied by pygmy rabbits in Utah with particular attention given to factors, such as sagebrush age, that have received only limited attention (Larrucea and Brussard 2008b). We hypothesized that pygmy rabbits would select taller and denser stands of sagebrush at locations with loamy soils compared to unoccupied sagebrush habitats. We predicted that, as a result of preference of pygmy rabbits for taller and denser stands of sagebrush, mean age of sagebrush in occupied habitat would be greater than that at unoccupied sites (Green and Flinders 1980, Himes and Drohan 2007, Larrucea and Brussard 2008b). This information will help identify characteristics of preferred habitat for pygmy rabbits in Utah and provide a better understanding of the ecological dynamics occurring within these habitats.

METHODS

Study Area

We collected habitat data between May 2005 and August 2010 at sites across the state of Utah (Fig. 1) within the known range of pygmy rabbits. Elevation at these sites ranged from 1494 m to 2686 m. Based on climate data from 8 weather stations, which we selected to represent the regional climates of our sites, mean minimum annual temperatures ranged from -4 to 6 °C, mean maximum annual temperatures ranged from 13 to 20 °C, and mean annual precipitation varied from 18 to 51 cm (Table 1; http://www.wrcc.dri.edu/summary/Climsmut.html).

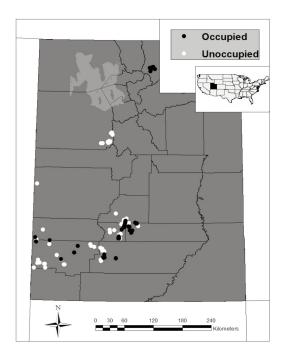


Fig. 1. Locations in Utah, USA, where we measured attributes of potential pygmy rabbit (*Brachylagus idahoensis*) habitat (i.e., sagebrush habitat) from 2005 to 2010. Black dots represent locations with active pygmy rabbit burrows, whereas white dots represent locations without active burrows.

All of the sites we sampled occurred in sagebrush habitats with upper hillsides dominated by either aspen (*Populous tremuloides*), juniper (*Juniperus* spp.), or pinyon pine (*Pinus edulis*). Lower elevations often consisted of wet, grassy valley bottoms typically used for agriculture or grazing.

Big sagebrush (A. tridentata) communities in our study area were occupied by numerous species including other lagomorphs that may compete with pygmy rabbits, such as blacktailed jackrabbits (Lepus californicus), cottontails (Sylvilagus spp.), and white-tailed jackrabbits (Lepus townsendii). Potential mammalian and avian predators of pygmy rabbits that occurred in these areas included badgers (Taxidea taxus), Bald Eagles (Haliaeetus leucocephalus), Barn Owls (Tyto alba), bobcats (Lynx rufus), coyotes (Canis latrans), Ferruginous Hawks (Buteo regalis), Golden Eagles (Aquila chrysaetos), Great-horned Owls (Bubo virginianus), Long-eared Owls (Asio otus), long-tailed weasels (Mustela frenata), Northern Harriers (Circus cyaneus), Prairie Falcons (Falco mexicanus), Common Ravens (*Corvus corax*), red foxes (*Vulpes vulpes*), Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*Buteo lagopus*), Short-eared Owls (*Asio flammeus*), and Swainson's Hawks (*Buteo swainsoni*).

Data Collection

We conducted this study in conjunction with a survey for pygmy rabbits throughout the state of Utah. This survey included investigation of areas where pygmy rabbits occurred historically and searches of areas where potential pygmy rabbit habitat had been identified (Janson 2002). Survey work included multiple walk transects in historic or potential habitat to determine if identified areas were occupied by pygmy rabbits. We identified occupied sites by presence of fresh burrows, pellets, and other evidence observed on walk transects (Larrucea and Brussard 2008a). Because pygmy rabbits spend most of their time in close proximity to burrows (i.e., within 100 m) and are considered central-place foragers (Rosenberg and McKelvey 1999, Heady and Laundré 2005), we used active burrows as the center points for habitat measurements at occupied sites (Sanchez et al. 2009). For comparison, we evaluated habitat characteristics at random locations within sagebrush areas (i.e., potentially suitable habitat) determined to be unoccupied during survey work.

At each occupied and unoccupied site, we collected habitat measurements that included vegetative cover, horizontal obscurity, percent understory composition, shrub density, and sagebrush decadence. For vegetative cover, we used the line-intercept method along 15-m transects in each cardinal direction from the burrow or a random point in unoccupied habitat. For horizontal obscurity measurements, we used a cover board with 36 squares (Bunnell et al. 2004). We placed the cover board at the burrow or random site, and then read the number of squares obscured by vegetation while kneeling down (to simulate height of a predator such as a covote) from distances of 2.5 m, 5 m, and 10 m in each cardinal direction. To determine percent composition of the understory, we used a 0.25-m² quadrat (Daubenmire 1959) placed at the center point (burrow or random location) and one random point along the 15-m transect in each cardinal direction (5 quadrats per site). Within each quadrat, we made an ocular estimate of percent moss, bare

TABLE 1. Mean temperature (°C), mean maximum temperature (°C), mean minimum temperature (°C), and mean annual precipitation (cm) from 8 weather stations (1981–2010) situated in close proximity to occupied and unoccupied pygmy rabbit (*Brachylagus idahoensis*) sample locations in Utah, USA, where we measured soil, vegetative, and topographic features from 2005 to 2010. Available from: http://www.wrcc.dri.edu/summary/Climsmut.html

County	Weather station (#)	Mean temp.	Max. temp.	Min. temp.	Precip.
Tooele	Tooele (428771)	11.83	17.94	5.78	51.00
Rich	Woodruff (29595)	4.33	13.00	-4.33	25.50
Sevier	Koosharem (424764)	6.94	16.17	-2.28	25.60
Millard	Eskdale (422607)	10.56	19.28	1.78	17.50
Iron	Modena (425752)	10.22	19.67	0.72	29.44
Garfield	Panguitch (426601)	5.94	15.94	-4.00	24.92
Piute	Angle (420168)	6.56	16.22	-3.17	22.76
Wayne	Loa (425148)	6.78	15.67	-2.17	20.14

ground, rock, litter, grasses, shrubs, trees, and forbs. We then calculated percent understory composition for each component at each site as the average of the 5 values from each plot. For sagebrush decadence, we made an ocular estimate of the percent of each sampled shrub that appeared dead (i.e., defoliated branches; Bunnell et al. 2004).

To measure distances from the burrow or random point to the nearest human structure, possible raptor perch, and habitat edge, we used a laser rangefinder. Human structures were defined as buildings, power lines, fences, etc. We defined habitat edges as transitions from sagebrush to nonsagebrush habitats (e.g., roads, meadows, previous fire scars, etc.). We also collected soil at each site in order to assess any potential differences in soil texture between occupied and unoccupied sites. We collected soil samples at a 15-cm depth and then submitted them to the Brigham Young University soils lab to determine percent clay, sand, and silt for each sample. To determine sagebrush age at occupied and unoccupied sites, we collected sagebrush core samples (Ferguson 1964, Perryman and Olson 2000) from 3 different plants at each site. After removal of a cross section, we sanded and wetted (if necessary) the sample so that growth rings were visible. We then counted the growth rings in order to estimate age of each plant. We also included a separate estimate of age that accounted for missing parts of a core. When core pieces were obviously missing, we calculated this estimate of age by assuming equal spacing of rings in parts of the cores that were missing.

We coupled the measurements collected at each site with GIS-based metrics of aspect, curvature, elevation, and slope. To derive GISbased measures of these features, we used ArcGIS version 10[®] (Esri Inc., Redlands, CA) and UTM coordinates of each sample location. We generated aspect, curvature, elevation, and slope variables using a 30-m DEM obtained from the Utah GIS portal (http://agrc.its.state .ut.us). To get a value that accurately represented aspect, we took the cosine and sine of our aspect values, which gave us northing and easting degree values that we could use in the final analysis. Because pygmy rabbits may select these habitat characteristics at multiple spatial scales, we generated buffers surrounding each location by using a 100-m, 500-m, and 1000-m radius. We chose these scales based on previous work suggesting that homerange areas of pygmy rabbits are small and that the impact of sagebrush removal extends to about 100 m (Sanchez and Rachlow 2008, Pierce et al. 2011, Edgel 2013). We then calculated the average value for each variable within each buffer and used these average values in statistical analyses. With information collected on the ground and the GIS-based metrics, we developed a list of 77 variables (Table 2) potentially useful in discriminating between occupied and unoccupied sites.

Data Analysis

To differentiate between occupied and unoccupied habitats, we used random forests (Cutler et al. 2007) in program R (R Development Core Team 2011). Random forests is a nonparametric classifier that builds multiple classification trees and then scrambles data for each explanatory variable in an iterative fashion to determine change in associated predictive ability for each variable. Compared to other classifiers (e.g., logistic regression or discriminant function analysis), random forests has high accuracy and the ability to model complex interactions. It also produces an estimate of

TABLE 2. Topographic, vegetative, anthropogenic/predator, and abiotic attributes used to discriminate between occupied and unoccupied pygmy rabbit (*Brachylagus idahoensis*) sites in Utah, USA, from 2005 to 2010.

Variable	Description		
Topographic			
Aspect	Measured at 0 (sampling center point), 100, 500, and 1000-m scales		
Curvature	Measured at 0 (sampling center point), 100, 500, and 1000-m scales		
Elevation	Measured at 0 (sampling center point), 100, 500, and 1000-m scales		
Slope	Measured at 0 (sampling center point), 100, 500, and 1000-m scales		
Vegetative			
Understory composition	Mean percent forbs, grasses, lichen, litter, moss, shrubs, non-sagebrush shrubs,		
	and sagebrush from 0.25 -m ² Daubenmire quadrats $(n = 5)$ at each site		
Sagebrush height	Mean height of 3 sagebrush plants sampled at each site		
Sagebrush width	Mean width of 3 sagebrush plants sampled at each site		
HO	Mean horizontal obscurity measured at 2.5, 5, and 10 m		
Percent HO	Percent horizontal obscurity measured at 2.5, 5, and 10 m		
Sagebrush age	Mean age, maximum age, and minimum age of sagebrush		
Sagebrush decadence	Mean percent decadence of 3 sagebrush sampled at each site		
Vegetation structure	Shrub height and canopy width of closest shrub to sampling point		
Shrub density	Number of shrubs rooted within one quadrant of a circle with a 3-m radius		
% cover	Mean percent cover of forbs, grasses, moss, and shrubs from line transects		
% shrub decadence	Mean percent shrub (sagebrush) decadence		
Anthropogenic/predator			
Distance edge	Distance (m) from sampling point to human and natural edge		
Distance structure	Distance (m) from sampling point to nearest human structure		
Distance raptor perch	Distance (m) from sampling point to nearest raptor perch		
Distance cliff	Distance (m) from sampling point to nearest cliffs		
Distance road	Distance (m) from sampling point to nearest road or off-road-vehicle trail		
Abiotic			
Soil composition	Percent clay, sand, and silt from 15 cm depth		
RSC	Rock size class value at sampling point		
% rock	Mean percent rock from 0.25 -m ² Daubenmire quadrats ($n = 5$) at each site		
% bare ground	Mean percent bare ground from 0.25 -m ² Daubenmire quadrats ($n = 5$) at each s		

variable importance (MDA; mean decrease in accuracy) that is not affected by multicollinearity (Cutler et al. 2007). To assess prediction accuracy, random forests computes an out-of-bag (OOB) error rate by withholding approximately one-third of the data. We considered mean decreases in accuracy above 1.0 to be indicative of influential variables that successfully discriminated between occupied and unoccupied habitats. After identifying variables with the greatest ability to differentiate between occupied and unoccupied sites, we plotted means and confidence intervals (CI) for these variables by site type (occupied or unoccupied) to determine effect sizes (strength and direction).

RESULTS

We sampled 133 sites in Utah between May 2005 and August 2010 (Fig. 1) to include 72 occupied and 61 unoccupied by pygmy rabbits. We did not identify any unoccupied sites in Rich County (northern Utah), as all of the areas we sampled within sagebrush had evidence of pygmy rabbits (i.e., pygmy rabbit

pellets). In contrast, despite historic evidence of pygmy rabbits and seemingly suitable habitat, we found no evidence of pygmy rabbits in the areas we sampled in Tooele County (central Utah). In southern Utah, occupied and unoccupied sites occurred in roughly equal proportion (Fig. 1).

Eleven of the 77 variables (Table 2) had a mean decrease in accuracy (MDA) of 1.0 or greater (Fig. 2). The variable with the greatest ability to differentiate between occupied and unoccupied sites was horizontal obscurity (Fig. 2). Elevation was also important, with an MDA above 1.0 for measurements at all 3 scales (Fig. 2). Percent understory composed of shrubs and sagebrush and percent decadence of sagebrush were additional variables with MDAs above 1.0 (Fig. 2). The "out of bag" (OOB) estimate of error rate was 6.77%.

Differences in mean horizontal obscurity between occupied and unoccupied sites were greatest near the burrow (2.5 m and 5 m). At shorter distances (2.5 m and 5 m), mean horizontal obscurity values were almost twice as large at occupied sites compared to unoccupied

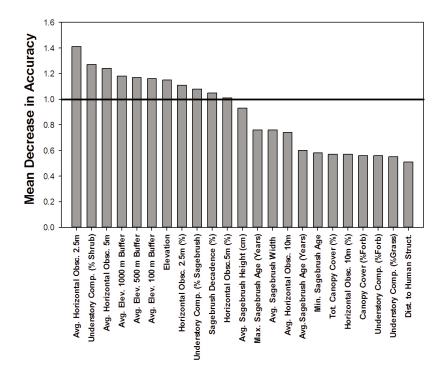


Fig. 2. Ranking of habitat variables used to discriminate between occupied and unoccupied pygmy rabbit (*Brachylagus idahoensis*) habitat in Utah, USA, from 2005 to 2010. Represented are the most influential 23 variables on the *x*-axis (descending order) and their associated mean decrease in accuracy (MDA) on the *y*-axis from an analysis using random forests. MDAs above 1.0 are typically considered good discriminants.

sites (Fig. 3). Similarly, understory composition at occupied sites included a higher mean percent composition of total shrubs and sagebrush than at unoccupied sites (Fig. 3). Elevation at occupied sites was also greater than at unoccupied sites, whereas sagebrush decadence was lower at occupied sites in relation to unoccupied sites (see Fig. 3).

Sagebrush age was not included in the list of variables with an MDA of 1.0 or greater (Fig. 2). Sagebrush maximum age (incorporating estimates from cores missing from sagebrush samples) had the highest MDA for age-related variables, with a value of 0.76. Estimated ages at occupied sites were greater than estimates from unoccupied sites, but confidence intervals overlapped. Mean maximum age of sagebrush at occupied sites was 42.30 years (95% CI 38.88-45.72) compared to 39.64 years (95% CI 36.54–42.74) at unoccupied sites. However, the average minimum age at occupied sites was 23.98 years. Similar to age, soil textures had limited predictive ability, with MDAs < 0.25. Mean soil composition at occupied sites was 0.44 sand (95% CI 0.40–0.47), 0.31 silt (95% CI 0.29–0.34), and 0.25 clay (95% CI 0.23–0.27) compared to 0.44 sand (95% CI 0.41–0.48), 0.30 silt (95% CI 0.27–0.32), and 0.26 clay (95% CI 0.24–0.28) at unoccupied sites. Similarly, we found no evidence that distance to human structure, distance to natural and human edges, or distance to raptor perches differed between occupied and unoccupied sites.

DISCUSSION

Horizontal cover measured 2.5 m and 5 m from the burrow site was best able to discriminate between occupied and unoccupied habitats in our sample. Mean obscurity at these distances for occupied sites was nearly double that observed at unoccupied sites (Fig. 3). The majority of this horizontal obscurity was shrub cover from sagebrush. These findings are consistent with results from California, Idaho, Nevada, Oregon, and Wyoming, which have also identified shrub cover as an important variable in site selection (Green and Flinders 1980, Weiss and Verts 1984, Katzner and Parker

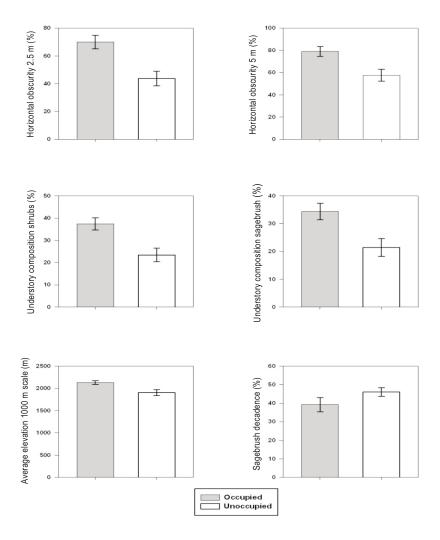


Fig. 3. Mean values for variables identified as important discriminants (random forests mean decrease in accuracy >1.0) of occupied and unoccupied pygmy rabbit (*Brachylagus idahoensis*) habitat in Utah, USA, from 2005 to 2010. Whisker bars represent the 95% confidence intervals.

1997, Larrucea and Brussard 2008b). In Nevada, islands of taller sagebrush and stands that provided greater cover could be used to identify sites where pygmy rabbits were likely to occur (Larrucea and Brussard 2008b). We also observed similar pockets of tall, dense sagebrush associated with occupied sites.

Interestingly, however, this selection for greater amounts of cover was not related to sagebrush age across the scale we evaluated (average age of sagebrush at occupied sites ranged between 23.98 and 42.30 years). Sagebrush age was low on the importance plot (Fig. 2), with an MDA of 0.76 for maximum age. Moreover, we found significant overlap in con-

fidence intervals around mean estimates of age for occupied and unoccupied sites. Greater amounts of cover at occupied sites, therefore, is more likely attributed to factors other than age. These factors may include variation in soil nutrients, water availability, or other factors facilitating growth and creating greater amounts of cover. Preliminary work in Nevada supports this interpretation for sagebrush ages; however, sample size was limited to only 7 sites (Larrucea and Brussard 2008b). It is possible that pygmy rabbits positively influence growth of sagebrush near burrows due to nutrient input (feces, urine) and soil aeration (digging); however, these ideas remain untested and need

further work. Nonetheless, because average minimum sagebrush age at occupied sites was 23.98 years, we suggest that at least 2 decades of sagebrush growth in our climatic region may be required following a disturbance such as fire or sagebrush manipulation before sagebrush habitats are again suitable for pygmy rabbits.

We found sagebrush at occupied sites to be less decadent (i.e., fewer dead or defoliated branches; Bunnell et al. 2004) than at unoccupied sites (Fig. 3). This finding could be an indicator that in unoccupied areas, sagebrush has reached levels of decadence no longer suitable for pygmy rabbits. Increased levels of sagebrush decadence also likely decrease cover and reduce available food resources, as sagebrush constitutes a majority of pygmy rabbit diet throughout the year (Green and Flinders 1980). Managers should make decisions that promote the health of a diverse stand of sagebrush plants, including recruitment of new plants and preservation of dense stands of sagebrush that provide sufficient cover for pygmy rabbits.

Soil textures at occupied and unoccupied sites were very similar, with no difference in percent sand, silt, or clay. We measured only unoccupied sites within sagebrush steppe habitat that apparently had soil texture similar to occupied sites. The mean values we observed for soil texture were also very similar to those found in Nevada (0.39 sand, 0.41 silt, and 0.20 clay) and Oregon (0.50 sand, 0.27 silt, and 0.23 clay) (Weiss and Verts 1984, Larrucea and Brussard 2008b). A study done in Idaho, however, reported a higher proportion of sand than we found in Utah, with soils containing 0.81 sand, 0.14 silt, and 0.05 clay (Gabler et al. 2001). Our results and the variation in the values reported above suggest that soil texture is unlikely to help in predicting pygmy rabbit presence within sagebrush communities at a fine scale. Perhaps other measures such as soil depth would provide more information than texture. These results are consistent with predictive habitat modeling efforts that often are successful in identifying nonhabitat based on vegetation attributes (e.g., presence of sagebrush) but show weaknesses in predicting occupied habitat within sagebrush (Gabler et al. 2000, Rachlow and Svancara 2006).

Elevation at all 3 scales ranked highly, with MDAs > 1.0 (Fig. 2). We consistently observed higher mean elevations for occupied sites in

comparison to the nearest unoccupied sites at all spatial scales (Fig. 3). In Nevada, a shift in pygmy rabbit habitat to higher elevations over the last few decades was reported—ostensibly due to warmer temperatures at lower elevations (Larrucea and Brussard 2008c). Increased temperatures may reduce the availability of snowpack for winter burrows, thus resulting in higher predation pressure and reduced access to food sources. Another possible explanation for our findings may be that with climatic change and warming at lower elevations, average summer temperatures are too high for pygmy rabbits. Pygmy rabbits are related to pikas (Ochotona princeps), which are sensitive to temperature changes (Beever et al. 2003, Grayson 2005, Galbreath et al. 2009). Alternatively, poor sagebrush health or size at lower elevations could also explain this relationship. Further work should be conducted to evaluate thermal suitability of habitat for pygmy rabbits and possible implications of climate change on this species.

It is apparent from our study and others that the future of pygmy rabbits is directly connected with the loss, degradation, and fragmentation of sagebrush habitats (Thines et al. 2004, Grayson 2006, Shipley et al. 2006, Pierce et al. 2011). Given the multitude of threats to sagebrush habitats, it is essential that proactive management decisions be made that will mitigate impacts to pygmy rabbits and promote long-term conservation of sagebrush habitats (Barney and Frischknecht 1974, Thines et al. 2004, Bradley 2010). If we are to conserve pygmy rabbits in Utah and throughout their range, it will be essential to protect and maintain healthy sagebrush habitats.

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LITERATURE CITED

Baker, M.F., R.L. Enc, J.S. Gashwiler, M.H. Schroeder, and C.E. Braun. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bulletin 88:165–171. Barney, M.A., and N.C. Frischknecht. 1974. Vegetation changes following fire in the pinyon-juniper type of

- west-central Utah. Journal of Range Management 27:91–96.
- BEETLE, A.A. 1960. A study of sagebrush. The section *Tridentatae* of *Artemisia*. Bulletin 368. Wyoming Agricultural Experimental Station 368:1–83.
- Beever, E.A., P.F. Brussard, and J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy 84:37–54.
- Bradley, B.A. 2010. Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use, and invasive species in Nevada, USA. Ecography 33:198–208.
- Braun, C.E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.
- Braun, C.E., O.O. Oedekoven, and C.L. Aldridge. 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Transactions of the North American Wildlife and Natural Resources Conference 67:337–349.
- Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677–688.
- Bunnell, K.D., J.T. Flinders, D.L. Mitchell, and J.H. Warder. 2004. Occupied and unoccupied sage grouse habitat in Strawberry Valley, Utah. Journal of Range Management 57:524–531.
- Crow, C., and C. van Riper III. 2010. Avian community responses to mechanical thinning of a pinyon-juniper woodland: specialist sensitivity to tree reduction. Natural Areas Journal 30:191–201.
- CUTLER, D.R., T.C. EDWARDS, K.H. BEARD, A. CUTLER, AND K.T. HESS. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.
- D'ANTONIO, C.M., AND P.M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 50:43–64.
- DOBLER, F.C., AND K.R. DIXON. 1990. The pygmy rabbit (*Brachylagus idahoensis*). Pages 111–115 in J.A. Chapman and J.E.C. Flux, editors, Rabbits, hares and pikas. Status survey and conservation action plan. IUCN, Gland, Switzerland.
- EDGEL, R. 2013. Habitat selection and response to disturbance by pygmy rabbits in Utah. Master's thesis, Brigham Young University, Provo, UT.
- EVANS, M., AND K. ROLLINS. 2008. Rangeland fires and cheatgrass: values at risk and support for preservation. Rural Connections 2:7–8.
- FERGUSON, C.W. 1964. Annual rings in big sagebrush (*Artemisia tridentata*). Papers of the Laboratory of Tree-Ring Research, University of Arizona Press, Tucson, AZ. 95 pp.
- Gabler, K.I., L.T. Heady, and J.W. Laundré. 2001. A habitat suitability model for pygmy rabbits (*Brachylagus idahoensis*) in southeastern Idaho. Western North American Naturalist 61:480–489.
- Gabler, K.I., J.W. Laundré, and L.T. Heady. 2000. Predicting the suitability of habitat in southeast Idaho for pygmy rabbits. Journal of Wildlife Management 64:759–764.

- GAHR, M.L. 1993. Natural history, burrow habitat and use, and home range of the pygmy rabbit (*Brachylagus idahoensis*) of Sagebrush Flat, Washington. Master's thesis, University of Washington, Seattle, WA.
- GALBREATH, K.E., D.J. HAFNER, AND K.R. ZAMUDIO. 2009. When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, Ochotona princeps). Evolution 63:2848–2863.
- Grayson, D.K. 2005. A brief history of Great Basin pikas. Journal of Biogeography 32:2103–2111.
- . 2006. The Late Quaternary biogeographic histories of some Great Basin mammals (western USA). Quaternary Science Reviews 25:2964–2991.
- GREEN, J.S., AND J.T. FLINDERS. 1980. Habitat and dietary relationships of the pygmy rabbit. Journal of Range Management 33:136–142.
- HEADY, L.T., AND J.W. LAUNDRÉ. 2005. Habitat use patterns within the home range of pygmy rabbits (Brachylagus idahoensis) in southeastern Idaho. Western North American Naturalist 65:490–500.
- HIMES, J.G., AND P.J. DROHAN. 2007. Distribution and habitat selection of the pygmy rabbit, *Brachylagus idahoensis*, in Nevada (USA). Journal of Arid Environments 68:371–382.
- INGELFINGER, F., AND S. ANDERSON. 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. Western North American Naturalist 64:385–395.
- JANSON, R.G. 2002. The pygmy rabbit from Utah to Montana: pygmy rabbit habitat in Montana. University of Montana, Cooperative Wildlife Research Unit, Missoula, MT. iii + 41 pp.
- KATZNER, T.E., AND K.L. PARKER. 1997. Vegetative characteristics and size of home ranges used by pygmy rabbits (*Brachylagus idahoensis*) during winter. Journal of Mammalogy 78:1063–1072.
- LARRUCEA, E.S., AND P.F. BRUSSARD. 2008a. Efficiency of various methods used to detect presence of pygmy rabbits in summer. Western North American Naturalist 68:303–310.
 - . 2008b. Habitat selection and current distribution of the pygmy rabbit in Nevada and California, USA. Journal of Mammalogy 89:691–699.
- 2008c. Shift in location of pygmy rabbit (Brachy-lagus idahoensis) habitat in response to changing environments. Journal of Arid Environments 72: 1636–1643.
- LYMAN, R.L. 1991. Late Quaternary biogeography of the pygmy rabbit (*Brachylagus idahoensis*) in eastern Washington. Journal of Mammalogy 72:110–117.
- . 2004. Biogeographic and conservation implications of Late Quaternary pygmy rabbits (Brachylagus idahoensis) in eastern Washington. Western North American Naturalist 64:1–6.
- MCALLISTER, K.R., AND W.M. PROGRAM. 1995. Washington State recovery plan for the pygmy rabbit. Washington Department of Fish and Wildlife, Olympia, WA. 73 pp.
- MILLER, R.F. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.
- MILLER, R.F., AND L. EDDLEMAN. 2000. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Technical Bulletin 151, Oregon State University Agricultural Experiment Station, Corvallis, OR. 35 pp.
- PERRYMAN, B.L., AND R.A. OLSON. 2000. Age-stem diameter relationships of big sagebrush and their management

- implications. Journal of Range Management 53: 342–346.
- Pierce, J., R. Larsen, J. Flinders, and J. Whiting. 2011. Fragmentation of sagebrush communities: does an increase in habitat edge impact pygmy rabbits? Animal Conservation 14:314–321.
- R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from: http://www.rproject.org
- 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.
- REYNOLDS, H. 1974. Habitat research . . . cornerstone in management. New Mexico Wildlife 19:28–30.
- ROBERTS, H.B. 2003. Status of the pygmy rabbit (*Brachylagus idahoensis*) in Idaho. Idaho Bureau of Land Management Technical Bulletin 03-6. 19 pp.
- ROSENBERG, D.K., AND K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63:1028–1038.
- SANCHEZ, D.M., AND J.L. RACHLOW. 2008. Spatio-temporal factors shaping diurnal space use by pygmy rabbits. Journal of Wildlife Management 72:1304–1310.
- SANCHEZ, D.M., J.L. RACHLOW, A.P. ROBINSON, AND T.R. JOHNSON. 2009. Survey indicators for pygmy rabbits: temporal trends of burrow systems and pellets. Western North American Naturalist 69:426—436.
- SCHNEEGAS, E.R. 1967. Sage grouse and sagebrush control. Transactions of the North American Wildlife and Natural Resources Conference 32:270–274.
- SHIPLEY, L.A., T.B. DAVILA, N.J. THINES, AND B.A. ELIAS. 2006. Nutritional requirements and diet choices of the

- pygmy rabbit (*Brachylagus idahoensis*): a sagebrush specialist. Journal of Chemical Ecology 32:2455–2474.
- THINES, N.J.S., L.A. SHIPLEY, AND R.D. SAYLER. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). Biological Conservation 119:525–534.
- [USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 2003. Endangered and threatened wildlife and plants; final rule to list the Columbia Basin distinct population segment of the pygmy rabbit (*Brachylagus idahoensis*) as endangered. Federal Register 68:10388–10409.
- VALE, T.R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. Journal of Range Management 28:32–36.
- WALKER, B.L., D.E. NAUGLE, AND K.E. DOHERTY. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.
- Weiss, N.T., and B.J. Verts. 1984. Habitat and distribution of pygmy rabbits (*Sylvilagus idahoensis*) in Oregon. Great Basin Naturalist 44:563–571.
- WHITE, S.M., J.T. FLINDERS, AND B.L. WELCH. 1982. Preference of pygmy rabbits (*Brachylagus idahoensis*) for various populations of big sagebrush (*Artemisia tridentata*). Journal of Range Management 35: 724–726.
- WILSON, T.L., J.B. ODEI, M.B. HOOTEN, AND T.C. EDWARDS. 2010. Hierarchical spatial models for predicting pygmy rabbit distribution and relative abundance. Journal of Applied Ecology 47:401–409.

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