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HABITAT SELECTION AND CURRENT DISTRIBUTION OF THE PYGMY RABBIT IN NEVADA AND CALIFORNIA, USA

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We surveyed the historic range of pygmy rabbits (*Brachylagus idahoensis*) in Nevada and California using infrared-triggered cameras to determine the species' current distribution and habitat selection. Areas with potential habitat were mapped using geographical information system coverages for elevation, big sagebrush (*Artemisia tridentata*) vegetation, and loamy soils. Within this region random sites and field-selected sites with sagebrush islands (prominent clusters of sagebrush higher than the surrounding sagebrush) were surveyed for the presence of pygmy rabbits. Sites were measured for sagebrush height, surrounding sagebrush height, sagebrush cover, and soil composition. Likelihood of pygmy rabbit occupancy at a site increased with the presence of sagebrush islands, increasing sagebrush cover, and decreasing surrounding sagebrush height. Additionally, we surveyed 1,394 other sites across the species' historic range and found current activity of pygmy rabbits at 258 of these sites. We measured sagebrush cover, sagebrush height, understory stem density, and presence or absence of cottontail rabbits, jackrabbits, red soils, cheatgrass, and rodent burrows at 454 sites. We used 80% of the data to create a logistic regression model. The top-ranked Akaike's information criterion–selected model suggested that likelihood of pygmy rabbit occupancy at a site increased with increasing sagebrush cover, decreasing understory stem density, absence of cottontails, absence of reddish soils, absence of cheatgrass, and absence of rodent burrows. This model showed a 79% accuracy rate in predicting occupancy within the remaining data. Current populations of pygmy rabbits were found throughout all of the species' historic range in Nevada and the southern portion of its range in California.

Key words: *Artemisia tridentata*, *Brachylagus idahoensis*, Great Basin, pygmy rabbit, remote camera, sagebrush

Sagebrush communities are decreasing in extent due to urbanization, agricultural conversion, and wildfires, while remaining stands are being degraded by excessive livestock grazing, fire management practices, and the invasion of alien weeds (Knick and Rotenberry 2001). One result of this loss and fragmentation is that many species dependent on sagebrush are in decline (Connelly et al. 2000). This may be especially true for species that are sagebrush obligates such as the pygmy rabbit (*Brachylagus idahoensis*).

Pygmy rabbits are the smallest leporids in North America, weighing only about 400 g and measuring 27 cm in total length (Wilde 1978). Big sagebrush (*Artemisia tridentata*) accounts for the majority of their diet and may comprise up to 99% of their diet in winter (Green and Flinders 1980). Sagebrush canopy also is important as cover for protection from predators (Grinnell et al. 1930). Additionally, the pygmy rabbit is 1 of only 2 species of rabbits in North America that digs its own burrows (Orr 1940). Because of the combination of these needs, pygmy rabbits are dependent on dense sagebrush growing on deep, friable soils (Weiss and Verts 1984). These specific habitat requirements mean that even a large, continuous stand of sagebrush may be highly fragmented for pygmy rabbits (Heady 1998).

Because of population declines in Oregon and Washington (Dobler and Dixon 1990; Thines et al. 2004) and a lack of solid information about its status elsewhere, the pygmy rabbit was designated as a Federal species of special concern and is currently listed as a Category 2 species by the United States Fish and Wildlife Service. A petition to change the listing throughout the entire Great Basin to threatened or endangered under the Endangered Species Act was filed in 2003 (Fite et al. 2003). In 2005, it was concluded that insufficient data were available to assess the current distribution of the species (Federal Register 2005). The status of the species is currently under review (Federal Register 2007).

Although the general habitat requirements of pygmy rabbits are well described (e.g., Janson 1946; Weiss and Verts 1984), it is also well documented that pygmy rabbits are difficult to locate and are not found in all areas within this general habitat type (e.g., Bradfield 1975; Janson 1946). This makes surveys for the species difficult. Studies conducted in Idaho have used

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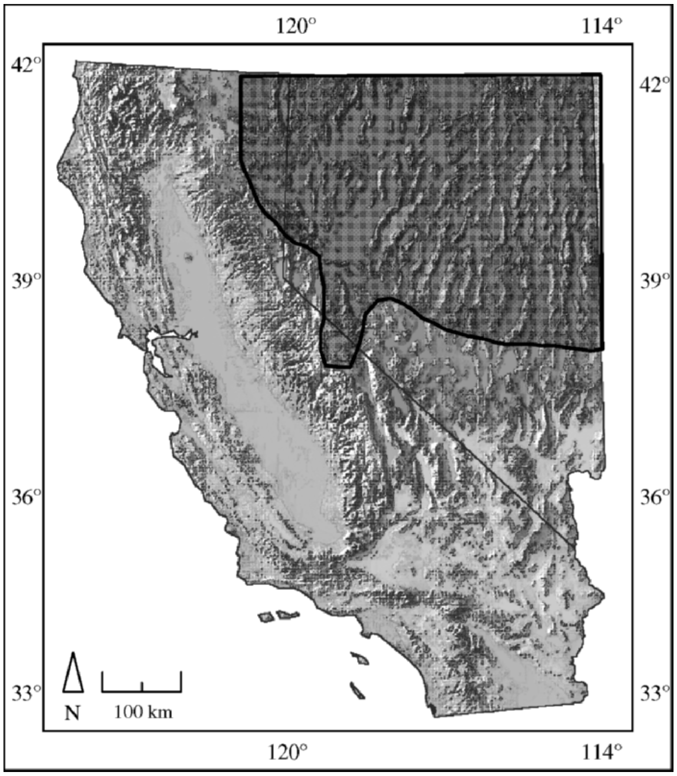

Fig. 1.—Boundary of the historic range of pygmy rabbits in Nevada and California, adapted from Hall (1946).

modeling to predict habitat for pygmy rabbits before conducting field surveys (Gabler et al. 2000; Rachlow and Svancara 2006). These macroscale models have included vegetation, slope and aspect, soils, and fire history with resulting probabilities of 57% (Gabler et al. 2000) and 65% (Rachlow and Svancara 2006) of predicting areas occupied by pygmy rabbits. Additional accurate information on habitat selection by pygmy rabbits will enhance modeling and survey efforts in the future.

Although Nevada encompasses the greatest portion of the historic range of pygmy rabbits, very little is known about the species' current status in the state. Most available information comes from broad mammalian surveys done in the 1930s (Hall 1946), although Himes and Drohan (2007) conducted a more recent survey in the extreme southeastern portion of the state. Pygmy rabbits in Nevada and California face similar problems with habitat degradation as do populations in Oregon and Washington (Connelly et al. 2000). Hence, determination of the status of the pygmy rabbit in these states is overdue.

This study examined vegetative and soil characteristics as well as faunal associates of sites that were occupied and unoccupied by pygmy rabbits to provide detailed information on the species' microhabitat selections in Nevada and California. We used these data to create a model that will allow surveys for active sites to be conducted more efficiently.

Materials and Methods

The study area for this project included portions of the states of Nevada and California within the historic range of pygmy rabbits (Fig. 1). This included Washoe, Humboldt, Pershing, Lander, Eureka, Elko, Churchill, White Pine, and portions of Nye, and Lincoln counties in Nevada and portions of Mono, Lassen, and Modoc counties in California. The area encompassed by the historic range in these 2 states is 22.1 million hectares.

Vegetation in this region is basin and range high desert. Elevations range from the lowest basins at about 920 m above sea level to several peaks above 3,600 m. Major plant communities include sagebrush, salt desert scrub, and pinyon–juniper woodlands. Precipitation across the region varies from 14 to 24 cm annually.

We 1st performed a macroscale spatial analysis to determine areas with potential habitat for pygmy rabbits in Nevada and California. We used the historic distribution for the pygmy rabbit according to Hall (1946) as our boundary (Fig. 1). We next obtained geographical information system coverages for elevation (30 m digital elevation model [DEM], United States Geological Survey), soils (State Soil Geographic [STATSGO] Database, United States Department of Agriculture; 1:250,000), and vegetation (Gap Analysis Program [GAP], United States Geological Survey; 1:24,000). Historic records of pygmy rabbits in Nevada and California ranged in elevation from 1,524 to 2,552 m. Therefore, we selected potential habitat for pygmy rabbits as any falling between 1,500 and 2,600 m in elevation. Further restrictions included areas described as having loamy soils as well as Wyoming big sagebrush (*A. t. wyomingensis*), basin big sagebrush (*A. t. tridentata*), or mountain big sagebrush (*A. t. vaseyana*).

Sagebrush islands.—Sagebrush islands are prominent clusters of sagebrush higher than the surrounding sagebrush. Other studies have noted that pygmy rabbits were more likely to be found in these clusters (Grinnell et al. 1930; Orr 1940). To test the affinity of pygmy rabbits for these clusters, 40 random points within the mapped region of potential habitat were selected using Hawth's ArcGIS analysis tools (Beyer 2004). Another 40 sites within the mapped region that had islands of taller sagebrush were chosen nonrandomly in the field as we drove to the random sites, mostly on dirt 2-track roads that led to isolated ranches or mines. The random Universal Transverse Mercator coordinates or the centers of the sagebrush islands were used as the plot identifiers.

All 80 sites were surveyed during daylight hours for current activity of pygmy rabbits. Up to an hour was spent at each location looking for areas with pellets and burrows. Surveyed areas ranged in size from approximately 150 m^2 to 3,200 m^2. At the end of the survey, a Trailmaster 1550 remote infrared-triggered camera unit (Goodson and Associates Inc., Lenexa, Kansas) was set at the site to photograph any lagomorphs present. Cameras were set near burrows if they had been located; if not, they were set in a central dense sagebrush area. We used a pulse delay setting of 1, a camera delay of 2 minutes, and 200 ASA 24-exposure print film (Larrucea 2007). Cameras were left at the site for 1 week. These methods were approved by University of Nevada–Reno animal care and use protocol A03/04-13, and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Upon returning to sites to collect camera equipment, vegetation measurements and soil samples were obtained. Sampled areas were kept small in size (100 m^2) to determine the specific microhabitat characteristics of areas selected by pygmy rabbits. Samples were centered on the camera location (pygmy rabbit burrows or centrally located dense sagebrush). Sagebrush canopy cover and height were measured using the line intercept sampling method (Bauer 1943). Because no differences in preference for different subspecies of *A. tridentata* have been found (Weiss and Verts 1984; White et al. 1982), all subspecies were grouped together. At every site a transect grid was extended from the camera location. A baseline was measured 5 m due east and 5 m due west from this center point. At the endpoints and center of the baseline, a transect line extended 5 m in both directions perpendicular to the baseline. Along each transect line the length of intercept for each plant, as well as the height of each plant touched by the transect line, was measured. Sagebrush cover was calculated by summing all intercept lengths at a site and dividing by the total transect lengths for the percent cover in the plot. All sagebrush heights at a site were summed and divided by the total number of measured plants for an average height for the plot. To determine the height of surrounding sagebrush at the 40 island sites we measured an additional 10-m transect line next to the sagebrush clusters.

A soil sample from 5 cm beneath the surface was collected next to burrows if they had been located or otherwise at the center of the site. Samples were analyzed in the laboratory for particle size distribution using the hydrometer method (Rowell 1994). Once sand, silt, and clay content had been established, soils were classified to type using the United States Department of Agriculture soil texture triangle.

At the last 7 island sites sampled, a single sagebrush plant from within the island and a single plant from the surrounding area were sawed off at the base. We selected the plant with the largest basal circumference in the island and a representative plant from outside the island. A 10-cm section of each plant was taken back to the laboratory to determine age by counting growth rings. Sections were polished with sandpaper, and rings were counted using a hand lens.

Homoscedasticity of the data was tested using Mann–Whitney *U*-tests. Two-sample *t*-tests assuming equal variances were used to look for differences between random and island sites. We screened variables for correlation at $r > 0.5$. Multiple logistic regression was used to examine the relationship between presence or absence of pygmy rabbits and sagebrush density, canopy cover, sagebrush height, surrounding sagebrush height, and percent clay and sand content in soils. Competing models were evaluated using Akaike's information criterion corrected for small sample size (AIC_c—Burnham and Anderson 1998). AIC_c was used because the ratio of sample size divided by the number of parameters was less than 40 (Burnham and Anderson 1998).

Current distribution.—From 2003 to 2006 we opportunistically sampled additional areas with a combination of loamy soils and big sagebrush vegetation for current activity of pygmy rabbits. We focused our surveys on sites with sagebrush islands when they were present. Locations were mapped using a handheld global positioning system unit and surveyed using infrared-triggered camera methods (Larrucea and Brussard, in press). Cameras were placed at burrow sites or in dense sagebrush and left at each site for at least 1 week.

Sagebrush height and cover at these sites were recorded using the techniques described above. Understory stem density was measured using a 0.25-m^2 sampling frame. The frame was placed on the ground 4 times in random locations at each site, and all stems of grasses and forbs falling within the frame were counted. Total number of stems/m^2 was used so that sites could be assessed during different seasons. Understory stem density was placed into 6 categories ($0 = 0$–10 stems, $1 = 11$–40 stems, $2 = 41$–80 stems, $3 = 81$–140 stems, $4 = 141$–200 stems, $5 = >200$ stems). Visual estimates conducted at sites during 2004 before using frame counts showed a high correlation ($r = 0.97$); therefore, beginning May 2005, understory was assessed visually. We also noted the presence or absence of cottontail rabbits (*Sylvilagus*) and jackrabbits (*Lepus*) from the photographs. Additionally, we collected information on presence or absence of cheatgrass (*Bromus tectorum*), presence or absence of burrows of small rodents, and presence or absence of reddish soil color. Principal hue of soil color was determined using a Munsell soil color chart (MacBeth Division of Kollmorgen Instruments Corporation 1994, Baltimore, Maryland).

A propinquity analysis (Rappoport 1982) was done to look at the spatial relationships among known populations. This analysis consists of measuring the distance to each nearest neighboring location, and using the mean of the distance to each nearest neighboring point to draw a radius around each point. The general contour results in populated regions separated by distances larger than 2 arithmetic means. Survey locations and contour lines were mapped in program ArcView.

Variables were checked for correlation at $r > 0.5$ level. Variables then were entered into multiple logistic regression analyses, and competing models were evaluated using Akaike's information criterion (AIC—Burnham and Anderson 1998). We calculated the AIC weight, which provided a measure of the strength of evidence for each model. We calculated variable weights to describe the relative importance of each variable. Eighty percent of the data set was used to create the set of models, whereas 20% of the data was reserved to validate the top-ranked model.

Results

Sagebrush islands.—Geographical information system coverages overlaid with the historical range of pygmy rabbits, big sagebrush vegetation, loamy soils, and elevation resulted in identifying 7.9 million hectares of potential habitat for pygmy rabbits in Nevada and California. We generated random points for our survey locations within this region. Nine locations had to be rejected because of lack of accessibility or on-site determination of inappropriate vegetation. Sites were excluded because of accessibility if lands were private and permission could not be obtained (3 locations) or if random points landed in extremely remote locations that would require more than

TABLE 1.—Akaike's information criterion corrected for small sample sizes (AIC_c) scores for data from island sites. We included all candidate models with Akaike weights that were within 10% of the highest in our confidence set as well as the null model. Competing models with $\Delta AIC_c < 2.0$ are shown with an asterisk. Model weights (ws) indicate the weight of evidence that each model is the best approximating model. Akaike parameter weights[a] were calculated by summing the weights for each model that contained the parameter of interest. Cover = sagebrush cover, Island = island site, Height = surrounding sagebrush height, Sand = sand content in soil.

Model	−Log-likelihood	k	AIC_c	ΔAIC_c	w
Island Cover Height	41.68	4	91.36	0.00*	0.38
Island Height	43.41	3	92.82	1.46*	0.18
Island Cover Height Sand	41.51	5	93.02	1.66*	0.17
Island Cover	43.75	3	93.50	2.14	0.13
Island Height Sand	43.41	4	94.82	3.46	0.07
Island	45.47	2	94.94	3.58	0.07
Null model	53.41	1	108.82	17.55	< 0.001

[a] Akaike parameter weights: Island = 1.00, Cover = 0.68, Height = 0.80, Sand = 0.24.

a day's hike from the nearest road (2 locations). Most sites were accessed by hiking from small, dirt 2-track roads. Sites also were removed if no sagebrush was present at the location (4 locations). Sagebrush was not present at the 4 sites because of recent fires. Nine new random points were generated to replace these sites.

We surveyed the 40 random sites as well as 40 selected sites with sagebrush islands for current activity of pygmy rabbits. We determined presence of pygmy rabbits from pellet and burrow surveys and confirmed findings with photographs. The photographs provided unequivocal evidence of pygmy rabbits at a site. Pygmy rabbits were found at 17.5% (7/40) of random sites and 60% (24/40) of selected sagebrush island sites ($\chi^2_1 = 15.22$, $P < 0.0001$).

Variables measured included sagebrush height at the survey locations, sagebrush height surrounding the survey locations, sagebrush cover, and soil consistency (Table 1). The mean difference in height of the sagebrush growing in islands and the surrounding sagebrush was 56 cm (range: 13–125 cm). Surrounding sagebrush height at random and selected sites was similar ($t = -1.01$, $d.f. = 78$, $P = 0.315$, mean difference: 26.15, $SE = 3.9$). Sagebrush cover was greater at selected island sites ($t = 3.65$, $d.f. = 78$, $P = 0.0005$, mean difference: 12.65, $SE = 1.95$). Sand and clay content were similar at both types of sites (sand: $t = -0.849$, $d.f. = 78$, $P = 0.398$; clay: $t = -1.66$, $d.f. = 78$, $P = 0.102$). Mean sand, silt, and clay content from all sites where pygmy rabbits were currently active are provided in Table 2. Current activity of pygmy rabbits was found in silty clay loam (10 sites), clay loam (6 sites), loam (6 sites), sandy loam (5 sites), silt loam (2 sites), and sandy clay loam (2 sites). Growth-ring counts from island clusters and from surrounding plants showed no difference in age ($t = -0.510$, $d.f. = 6$, $P = 0.629$). The mean age of sampled sagebrush was 24.2 years (range: 16–36 years).

The AIC_c model selection for probability of the presence of pygmy rabbits at random and selected sites resulted in 3 competing models with ΔAIC_c scores less than 2 (Table 1). Sagebrush height and island variables were correlated ($r = 0.62$), as were sand and silt ($r = 0.79$) and sand and clay ($r = 0.68$). Island and sand explained more of the variation in the data, so we therefore included only sand, island site, surrounding sagebrush height, and sagebrush cover in the analyses. We included all candidate models with Akaike weights that were within 10% of the highest in our confidence set (Royall 1997). The island variable appeared in all the models within this set.

The top-ranked AIC_c-selected model suggested that likelihood of occupancy by pygmy rabbits at a site increased with island presence, increasing sagebrush cover, and decreasing surrounding sagebrush height. Any model with a ΔAIC value within 2 of the top selected model is considered to be reasonable given the data (Burnham and Anderson 1998). The top-ranked model was 2.1 times more likely than the 2nd-selected model and 2.2 times more likely than the 3rd-selected model to be the best given the data (Table 1). Akaike importance weights for individual parameters indicated that an island site was the most plausible explanation for pygmy rabbit occurrence at a locality followed by surrounding sagebrush height and cover (Table 1). We calculated goodness of fit tests to assess the fit of the top-ranked model and found no evidence of lack of fit (Pearson $\chi^2 = 77.7$, $d.f. = 76$, $P = 0.423$; $G^2 = 82.7$, $d.f. = 76$, $P = 0.279$).

Current distribution.—We conducted surveys for pygmy rabbits at 1,394 additional sites across Nevada and California and documented current activity of pygmy rabbits at 258 sites (Fig. 2). The current distribution of active sites was similar to the historic distribution. We located active sites in all counties in Nevada within the historic range as well as in Mono County in California. However, we found no active sites in Modoc or Lassen counties in California. Propinquity analysis calculated a mean distance of nearest-neighboring points of 13.1 km. We used this as a radius around all sites known to have pygmy rabbits present, which showed connectivity mostly within individual valleys and mountain ranges (Fig. 3).

Because propinquity analysis is a product of the number of survey points and this study was conducted on a broad, statewide scale, we also created a larger radius of 30 km around sites known to have activity of pygmy rabbits. Examination of recent data has shown that pygmy rabbits can travel greater distances than originally thought, and they have been observed traversing through nontypical habitat (Gahr 1993; Katzner and Parker 1998). Green and Flinders (1980) reported travel of 2.5 km by an individual pygmy rabbit over the course of only 3 days. Although a single individual would not likely travel 30 km, the larger radius is warranted to allow for additional populations that were not surveyed because of the broad scale of the study. This 30-km radius around locations with activity of pygmy rabbits showed 3 main areas with populations of pygmy rabbits in Nevada and California (Fig. 3). Populations in Mono County, California, were 162 km from the closest known populations in Nevada.

Sagebrush height, sagebrush cover, understory stem density, and presence or absence of cottontails, jackrabbits, rodent burrows, reddish colored soils, and cheatgrass, were recorded

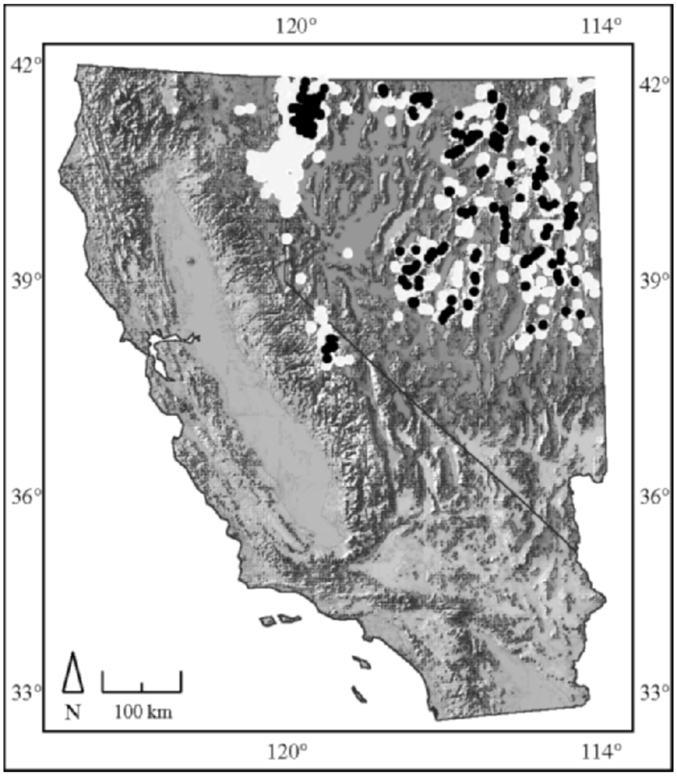

FIG. 2.—Map showing 1,474 locations surveyed from 2003 to 2006 for current presence of pygmy rabbits in Nevada and California. Photographs from infrared-triggered cameras provided unequivocal evidence of current activity. Currently occupied locations ($n = 258$) are shown in black, and locations where no pygmy rabbits were detected ($n = 1,216$) are shown in white. Locations where pygmy rabbits were present should be regarded as the minimum range of occurrence because this study was conducted on a large, statewide scale.

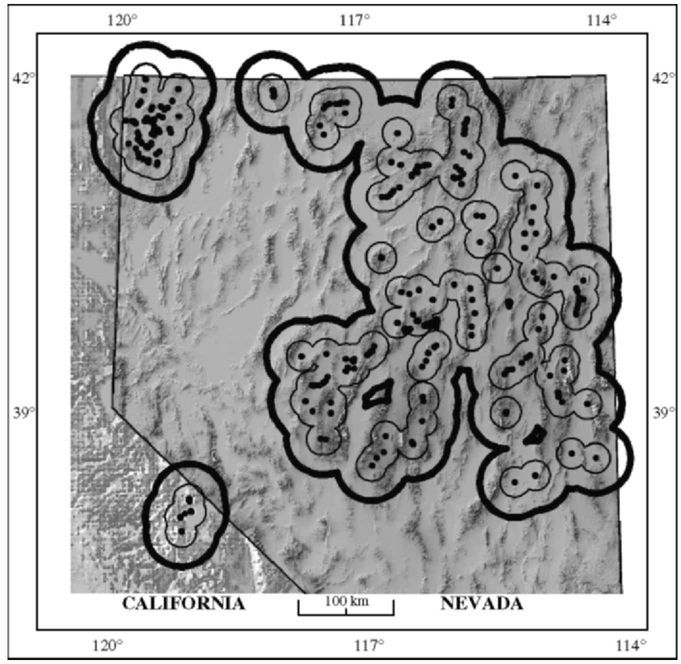

FIG. 3.—Propinquity analysis (Rappoport 1982) showing the potential connectivity of sites where pygmy rabbits are known to be present (points) in Nevada and California. Thin lines indicate a 13.1-km merged radius around known active locations. The thick line is a 30-km radius around active locations that suggests 3 regional populations of pygmy rabbits in Nevada and California. The populations at Mono Lake in California are separated from other known populations by 162 km.

at 454 of the surveyed sites. We collected soil samples from 9 sites with reddish soils. The sand and clay content of these reddish soils did not differ from that of soils analyzed from sites with current activity of pygmy rabbits (sand: $t = 0.568$, $d.f. = 16$, $P = 0.287$; clay: $t = 0.183$, $d.f. = 16$, $P = 0.428$). Means at occupied and unoccupied sites for sagebrush height, sagebrush cover, and soil measurements are provided in Table 2.

We used a random sample of 80% of the sites ($n = 364$) to create the logistic regression model. None of the variables was significantly correlated at $r > 0.5$. AIC model selection identified 4 models with $\Delta AIC < 2$. Sagebrush cover, understory stem density, presence of cottontails, presence of reddish soils, and presence of burrows appeared in all 4 of these models. The top-ranked model suggested that likelihood of the presence of pygmy rabbits at a site increased with increasing sagebrush cover, decreasing understory stem density, absence of cottontails, absence of reddish soils, absence of cheatgrass, and absence of rodent burrows (Table 3). This model was 1.2 times more likely than the 2nd-ranked model to be the best fit for the data. Akaike importance weights for individual parameters showed that sagebrush cover, presence or absence of cottontails, and understory stem density were the most plausible explanations for presence of pygmy rabbits at a site followed by rodent burrows, reddish soils, and cheatgrass (Table 3). Goodness of fit tests showed no evidence for lack of fit for the top-ranked model (Pearson $\chi^2 = 360.1$, $d.f. = 353$, $P = 0.386$; $G^2 = 317.5$, $d.f. = 443$, $P = 0.913$). The top-ranked model showed a 79% accuracy rate in predicting occupancy among the remaining 90 sites ($\chi^2 = 17.07$, $d.f. = 1$, $P < 0.0001$).

DISCUSSION

Current distribution.—The majority of studies on the pygmy rabbit have been conducted in the northern part of its range

TABLE 2.—Mean value ($\bar{X}$), standard error (*SE*), range, and the number of sites measured (*n*) for 5 habitat variables at sites that were occupied and unoccupied by pygmy rabbits in Nevada and California, 2003–2006.

	Variable	$\bar{X}$	*SE*	Range	*n*
Occupied	Sagebrush height (cm)	98.4	32.9	40–193	110
	Sagebrush cover (%)	44.8	17.6	11–93	110
	Sand content (%)	39.1	18.8	19–76	38
	Clay content (%)	20.4	10.6	6–33	38
	Silt content (%)	40.5	11.8	18–55	38
Unoccupied	Sagebrush height (cm)	92.4	37	20–203	344
	Sagebrush cover (%)	33.1	18.2	9–100	344
	Sand content (%)	43.4	18.2	18–78	58
	Clay content (%)	19.7	11.8	1–48	58
	Silt content (%)	37.2	14.5	8–76	58

Table 3.—Comparisons of various models using Akaike's information criterion (AIC) scores to predict occurrence of pygmy rabbits at a site. Competing models with ΔAIC < 2.0 are shown with an asterisk. We included all candidate models with Akaike weights that were within 10% of the highest in our confidence set (Royall 1997) as well as the null model. Model weights (*w*) indicate the weight of evidence that each model is the best approximating model given the data and the set of candidate models. Akaike parameter weights[a] were calculated by summing the weights for each model that contained the parameter of interest. Cov = sagebrush cover, Und = understory stem density, Cot = presence of cottontail rabbits, Red = presence of reddish soils, Cheat = presence of cheatgrass, Bur = presence of rodent burrows, Hgt = sagebrush height, Jack = presence of jackrabbits.

Model	−Log-likelihood	k	AIC	ΔAIC	*w*
Cot Cov Und Bur Red Cheat	197.37	11	416.74	0.00*	0.22
Cot Cov Und Bur Red	198.56	10	417.12	0.38*	0.18
Cot Cov Und Bur Red Cheat Jack	196.69	12	417.38	0.64*	0.16
Cot Cov Und Bur Red Cheat Hgt	197.34	12	418.68	1.94*	0.08
Cot Cov Und Red	200.38	9	418.76	2.02	0.08
Cot Cov Und Bur Cheat Hgt Jack	198.47	11	418.94	2.20	0.07
Cot Cov Und Bur	200.49	9	418.98	2.24	0.07
Cot Cov Und Bur Red Cheat Hgt Jack	196.68	13	419.35	2.61	0.06
Cot Cov Und Bur Red Hgt Jack	197.92	12	419.84	3.10	0.05
Cot Cov Und Red Cheat Hgt	198.94	11	419.88	3.14	0.04
Null Model	251.38	1	504.76	88.02	<0.01

[a] Akaike parameter weights: Understory = 1.00, Cover = 1.00, Cottontails = 1.00, Burrows = 0.89, Red soil = 0.87, Cheatgrass = 0.63, Jacks = 0.34, Height = 0.30.

(e.g., Wyoming [Katzner 1994], Idaho [Gabler et al. 2000], Oregon [Meisel 2006; Weiss and Verts 1984], and Washington [Gahr 1993]). Our study presents the 1st large-scale survey of the species in Nevada and California, which includes the southern extent as well as the greatest portion of its historic range. In contrast to reports of greatly reduced numbers (Dobler and Dixon 1990), we found that pygmy rabbits were still extant throughout all of their historic range in Nevada and the southern portion of their range in California (Fig. 2). Taken as a whole, the current range is still similar to what was delineated in the 1940s by Hall (1946).

Spatial analysis of known current locations of pygmy rabbits showed 3 main regions with pygmy rabbits within Nevada and California (Fig. 3). On this large, statewide scale the northwestern and eastern regions of Nevada are connected through known populations of pygmy rabbits in Oregon (Meisel 2006; Weiss and Verts 1984), creating a relatively continuous distribution. However, this does not mean that pygmy rabbits necessarily can disperse among all the populations in northern Nevada. Propinquity analysis showed connectivity mostly in individual valleys and mountain ranges (Fig. 3). Pygmy rabbits are relatively slow moving and require cover as protection from predators (Severaid 1950). Barriers such as dry playas and montane habitat, as well as agricultural fields, large burned areas, and urban areas may not provide protection; pygmy rabbits are unlikely to cross them successfully. Further research needs to be conducted to determine potential dispersal distances before the true connectedness among these populations can be assessed. Evidently the Mono County populations in California truly are isolated from other known populations because they are separated from the nearest known population by a distance of 162 km and unsuitable habitat. These pygmy rabbits are likely to have been isolated from more eastern populations since the end of the Pleistocene (Grayson 2006).

The one region that seems to have lost pygmy rabbits is Modoc and Lassen counties in northern California. Although the absolute absence of a species at a site is extremely difficult to determine (Diamond 1987), the camera techniques we employed have a fairly strong detection efficiency of 95% (Larrucea and Brussard, in press). Despite extensive surveys conducted in this area, no current activity was detected. The area is relatively low in elevation (1,220 m) and was on the extreme western edge of the historic distribution. The region includes only 3 historic sites (1 in Modoc County and 2 in Lassen County) where pygmy rabbits were collected in 1877 (Henshaw 1920) and 1926 (Grinnell et al. 1930). A peripheral area such as this would be highly subject to a range retraction if it were to occur.

Microhabitat selection.—According to the top-ranked model, likelihood of the presence of pygmy rabbits at a site increased with increasing sagebrush cover, decreasing understory stem density, absence of cottontails, absence of reddish soils, absence of cheatgrass, and absence of rodent burrows. This validated model included habitat variables that have been shown to be important in other regions as well as additional variables that have not been previously described.

Sagebrush.—It has been well established that pygmy rabbits require big sagebrush as a food source and as protection from predators (Orr 1940; Weiss and Verts 1984). We also found sagebrush cover to be an important variable, as evidenced by the high relative parameter weight (Tables 1 and 3). Mean sagebrush cover at occupied sites (44.7%) was similar to reports from Idaho (Green and Flinders 1980). In contrast, overall surrounding sagebrush height, which is often reported as an important factor (Heady et al. 2001; Meisel 2006), was not found to carry much weight in the overall model compared to the other variables (Table 3). Mean sagebrush height found at occupied sites (98.4 cm) was similar to heights reported from Oregon (84.4 cm—Weiss and Verts 1984), and greater than the 56.0 cm in Idaho (Green and Flinders 1980). Rather, pygmy rabbits were more likely to occupy sites with prominent clusters of higher than surrounding sagebrush, or sagebrush islands (e.g., Grinnell et al. 1930; Orr 1940). These sagebrush islands occurred in a wide range of surrounding sagebrush heights (range: 12–117 cm).

Closer analysis of these island sites showed that they not only had higher, prominent sagebrush but also had greater sagebrush cover. The greater sagebrush cover corresponds to findings in our overall model. Although we were using the visible evidence of difference in sagebrush height to identify these sites, the important factor at these sites for the pygmy rabbit may be the less obvious increase of sagebrush cover within the island. Outside of islands there was very little correlation between surrounding sagebrush height and sagebrush cover.

Islands of taller sagebrush may be remnant stands of older sagebrush in areas of younger sagebrush or they may be sagebrush of a similar age growing on deeper soils with greater water availability (Ellison 1960). Our analysis of sagebrush ages from islands and surrounding areas was preliminary, and the sample size was small ($n = 7$). However, these samples showed no difference in age, suggesting that deeper, better-watered soils may be the key factor. Further research is needed to confirm this hypothesis.

In winter, the prominent vegetative structure of these sagebrush islands allows drifting snow to accumulate on the leeward side (Katzner and Parker 1997). Pygmy rabbits are active year-round (Green and Flinders 1980), and when there is adequate snow on the ground they create tunnels under the snow connecting them to different sagebrush plants (Green 1978; Katzner 1994; Katzner and Parker 1997; Rauscher 1997). This provides them with access to food sources while protecting them from some of their predators. Therefore, greater sagebrush cover, a greater snow pack in winter, and potentially deeper soils may combine to make islands of taller sagebrush highly favorable habitat for pygmy rabbits.

Soils.—As has been noted in studies from other regions, pygmy rabbits were found to occupy sites with friable soils. Occupied sites were located on loamy-type soils with a mean sand and clay content of 39.1% and 20.4%, respectively. This sand content was slightly lower than reports from occupied sites in Oregon (sand: 50.2%, clay: 19.5% [Meisel 2006]; sand: 51.1%, clay 18.5% [Weiss and Verts 1984]) and much lower than was found at occupied sites in Idaho (sand: 87.5%, clay: 5.0% [Gabler et al. 2001]). The highest sand content recorded at an active site in our study was 76% in Mono County, California. Even in this region, burrows tended to be located in the loamy inclusions. Soils with sand content higher than 70% tended to be associated with rodent burrows, which may explain the negative association between rodent burrows and presence of pygmy rabbits. Pygmy rabbits often use their burrows for several years (Larrucea 2007), and soils with less sand and higher clay content would provide greater integrity for burrow persistence (Brady and Weil 2002).

Although loamy soils are unquestionably important, we found that loamy soils with a reddish tint were negatively associated with the presence of pygmy rabbits (pygmy rabbits were associated with reddish soils only once). The soil consistency at these sites was similar to the consistency found at occupied sites, and the reason for the negative association is unknown. Future research might look at differences in mineral components between the soils that could influence the taste or texture of sagebrush or examine potential differences in thermal properties.

Understory.—Increasing levels of understory stem density were negatively associated with current presence of pygmy rabbits at a site. This finding is in contrast to that of Weiss and Verts (1984), who found no difference in amount of understory between occupied and adjacent sites ($n = 21$). The discrepancy may be due to a difference in sample size or to the fact that we did not select adjacent sites but rather evaluated 454 independent sites. It is also possible that the composition of the understory differed between the studies and that this contributed to the variation in results.

The greater probability of occupancy by pygmy rabbits at sites with low (or no) understory may be due to a combination of factors. Pygmy rabbits may create areas with little understory by foraging for grasses and forbs close to their burrows. Small home ranges and a preference to stay under cover may produce areas cleared of vegetation similar to those created by brush rabbits (*Sylvilagus bachmani*—Chapman 1971). This clearing of understory can serve the additional benefit of reducing grasses that may restrict movements or vision of pygmy rabbits (Weiss and Verts 1984). Competition with cottontail rabbits also might influence this relationship. The larger cottontails may be in competition with pygmy rabbits for resources such as burrows (Gahr 1993; Thines et al. 2004). Cottontails seem to be more prevalent in areas with more understory. Although pygmy rabbits can subsist on virtually nothing but sagebrush (Green and Flinders 1980), they do eat grasses and forbs when they are available. A certain amount of grasses and forbs even may be required to keep populations healthy (Green 1978; Thines et al. 2004; Wilde 1978).

Cheatgrass presence also was negatively associated with current presence of pygmy rabbits at a site. Cheatgrass occurred both as a sole understory species as well as a minor component in diverse understories, and the variables of cheatgrass presence and understory stem density were therefore not highly correlated. Except for during a short period in the spring, cheatgrass is unpalatable and indigestible (Weiss and Verts 1984), and once cheatgrass becomes well established it can create dense root mats that may be difficult for pygmy rabbits to burrow into.

Mapping of known habitat preferences along with elevational restrictions provided 7.9 million hectares of potential habitat for pygmy rabbits in Nevada and California. This provided only a rough estimate of where pygmy rabbits might occur. Pygmy rabbits can occur in very small inclusions of soil and vegetation that would not be mapped in conventional surveys (Gabler et al. 2001; Meisel 2006). Hence, once general habitat mapping is completed, it is more efficient to select random sagebrush islands for field surveys rather than survey at random locations within the mapped area (stratified random sampling). We found that focusing on sagebrush islands was 3.4 times more effective for locating pygmy rabbits than using only general habitat mapping. Specific geographical information system models with random survey points are more appropriate for more mobile animals that select habitat at larger scales.

This survey determined that pygmy rabbits still are found throughout most of their historic range in Nevada and in the southern portion of their range in California. This provides an opportunity to manage for this species while it exists at levels not requiring federal protection. Our study provides information on the probability of pygmy rabbit presence at a site based on easily surveyed variables as well as microscale components that can help managers make more-informed decisions for management of pygmy rabbits in the future.

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