VEGETATIVE CHARACTERISTICS AND SIZE OF HOME RANGES USED BY PYGMY RABBITS (*BRACHYLAGUS IDAHOENSIS*) DURING WINTER

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We determined sizes of home ranges for pygmy rabbits in southwestern Wyoming and characterized the vegetation within and outside those areas used during winters of 1993 and 1994. Seventy percent of pygmy rabbits used more than one core area within their home range. Habitats within home ranges had less low ground cover and a greater number of wider, taller *Artemisia tridentata* than did adjacent non-used areas. Pygmy rabbits selectively used dense and structurally diverse stands of *A. t. tridentata,* which also accumulated more snow than areas of low use. Structure and diversity of vegetation above the snow's surface declined as the season progressed and depths of snow increased. The subnivean environment provided access to a relatively constant supply of food and provided protection from predators and thermal extremes. We suggest that size of home ranges used by pygmy rabbits is influenced more by amount of vegetative cover than by forage.

Key words: *Brachylagus idahoensis,* pygmy rabbit, home range, *Artemisia tridentata,* structure of habitat, use of habitat

The pygmy rabbit (*Brachylagus idahoensis*), one of the smallest leporids in the world (ca. 400 g), is endemic to the vegetative communities of western big sagebrush (*Artemisia tridentata*–Bradfield, 1975; Jansen, 1946; Wilde, 1978), and subsists almost entirely on that shrub during winter (Green and Flinders, 1980*a,* 1980*b*). Pygmy rabbits endure harsh winters throughout much of their range, despite their limited diet, small body size, and no known metabolic torpor or food-caching abilities. Small variations in vegetative structure may have significant impacts on behavior and feeding habits because these rabbits are such extreme specialists in sagebrush-dominated habitats. Numbers of pygmy rabbits are believed to be declining in most known populations (Dobler and Dixon, 1990). As a result, degradation and disappearance of areas of sagebrush-steppe have become a concern for their conservation (Dobler and Dixon, 1990; Holecheck, 1981).

Type and availability of habitats are critical determinants of size, stability, and success in populations of animals. The amount of space a mammal uses outside of the breeding season depends primarily on how easily it can meet energetic demands in a given area (McNab, 1963; Reiss, 1988). Consequently, size of home range has been related to both body size (McNab, 1963; Palomares, 1994; Swihart, 1986; Swihart et al., 1988) and metabolic requirements (Bresinski, 1983; Lindstedt et al., 1986; Reiss, 1988). Monitoring an animal's home range during the most stressful times of the year is needed to define constraints on survival (Lindstedt et al., 1986). Most research on pygmy rabbits, however, has been conducted during summer (Gahr, 1993; Green, 1978; Weiss and Verts, 1984); no detailed study has focused on habitat requirements during the critical months of winter.

We describe patterns of use of habitat by pygmy rabbits relative to size and shape of their home ranges, characterize the general vegetative structure of the habitat used during winter, and define vegetative characteristics of core areas used by rabbits in southwestern Wyoming.

Materials and Methods

We conducted the study on southwest facing slopes of Fossil Butte (2,000–2,200 m elevation) at Fossil Butte National Monument (41°50′N, 110°44′W) west of Kemmerer, Lincoln Co., Wyoming. Temperatures during the study (January through March of 1993 and 1994) ranged from −25 to 15°C (Katzner, 1994). Slopes ranged from 6 to 60%; soils are basic clays and silty clays (Glenn, 1974). Precipitation, much of which fell as snow, accumulated in draws and gullies on the hillside. Vegetation was dominated by patches of basin big sagebrush (*A. t. tridentata*) growing densely at sites with deep soils and greater accumulation of precipitation.

We established a 950- by 300-m grid, using steel stakes placed at 50-m intervals. Each stake (1.54 by 1.3 cm) was color-coded so that precise locations within the grid could be determined from compass sightings to the four nearest stakes. We analyzed these data using a BASIC program (QuickBasic version 4.5, Microsoft, Redmond, WA) modified from White and Garrott (1990).

Rabbits were captured with modified, double-door Tomahawk traps (15 by 15 by 60 cm) or wooden box traps (18 by 22 by 61 cm) in January and February each year. Traps were set in runways, near burrows, and in areas used frequently. All Tomahawk traps were wrapped in white, polyethylene sacks to provide protection from predators and thermal stress. Wooden nest boxes were attached to one end of several Tomahawk traps so that the traps could remain open through the night. Multiple types of bait (e.g., apples, alfalfa, carrots, turnips, and lettuce) were used; trapping success did not appear to be influenced by bait.

We recorded the sex of captured animals (Petrides, 1951), and marked individuals with ear tags and radiotransmitters before release. Ear tags were uniquely numbered and had colored, plastic washers (National Band and Tag Co., Newport, KY). Radiocollars (165 MHz band, CHP-1H, Telonics Co., Mesa, AZ) weighed 15 g including the 1.5-cm wide nylon-webbing strap and a 10-cm whip antenna. We used a hand-held receiver and yagi antenna (Model TR-2 receiver, Telonics, Mesa, AZ) to locate collared animals on the grid one to three times each day. We located individuals during daylight hours; daily locations were spaced in time to avoid autocorrelation (Swihart and Slade, 1985; Swihart et al., 1988). We calculated home ranges using the adaptive-kernel method (Worton, 1989) on data from winter only. More specifically, a 95% isopleth on the program CALHOME was used (J. Kie et al., in litt., CALHOME home-range analysis program). We correlated size of home ranges with number of observations to determine whether size of sample affected our estimates. Sizes of home ranges ($\bar{X} \pm SE$) were compared between the 2 years of the study with a Student's t-test on Log_{10}-transformed data (Sokal and Rohlf, 1981).

To identify general characteristics of habitats used by pygmy rabbits at a large scale, we randomly placed eight 50-m transects in the area where home ranges were found and in adjacent areas where rabbits were never observed. To define specific attributes of the sites used by rabbits within that general habitat, we sampled vegetation with and without snow on the ground. During winter, we established pairs of 20-m transects and placed one transect of each pair in an area frequently used by pygmy rabbits and the other in an adjacent area of low use (four pairs in 1993; seven pairs in 1994). After snowmelt, we randomly placed 124 transects of 10 m in length in core areas of home ranges. Each transect was classified based on extent of use by rabbits as high, medium, low, or no use. Hence, we increased intensity of sampling at the finer scales chosen by the rabbits; length of transects was correspondingly shorter to fit within core areas used by the animals. Details on specific sampling techniques and placement, spacing, and classification of transects are found in Katzner (1994).

We used the line-intercept technique to estimate percentage of cover of all shrubs on each transect (Becker and Crockett, 1973). After snowmelt, specific measurements on shrubs were limited to *A. tridentata* ≥13 cm in height (T. Cundy, in litt.; Yabann et al., 1985) and rooted within 0.5 m of the transect. When snow precluded assessing the location of roots and height

of shrubs, all canopies of sagebrush within or touching a 1-m wide belt were measured. The total number of living and dead shrubs was counted and living *A. tridentata* were identified to subspecies (Stevens and McArthur, 1974). We estimated the percentage of each shrub that was alive as an index of age and health. We measured maximum height of both living and dead components of the shrub, minimum height of the living component, and size of canopy (maximum width plus minimum width divided by two). Depth of snow was measured at 1-m intervals along transects during winter. We measured vertical density of the vegetative structure by placing a wooden pole (3.5 by 3.5 by 213 cm) at 0.5-m intervals along the transect and averaged all vegetative contacts in each 10-cm interval. This technique was similar to Wiens and Rotenberry (1981).

All variables were averaged for each transect and analyzed using SAS (SAS Institute, Inc., 1987). We used an analysis of variance (ANOVA) to test for differences between variables in areas used by rabbits and those not used by rabbits, and among levels of use within home ranges. A Scheffe's test was used to analyze differences among means of each transect by level of use. We also made a correlation matrix for all variables. We used a repeated-measures ANOVA to compare depths of snow taken at weekly intervals in 1993 on transects in areas of high and low use. Bonferonni confidence intervals compared differences in depth of snow between levels of use at each sampling time (Neter et al., 1990). Depths of snow in 1994, in areas of high and low use, were compared with a Student's *t*-test (Sokal and Rohlf, 1981). We used a *t*-test to compare the vertical profiles of vegetative structure between areas of use and no use, and ANOVA to compare vegetative profiles among different levels of use within home ranges. A significance level of $P \leq 0.05$ was assumed for all analyses.

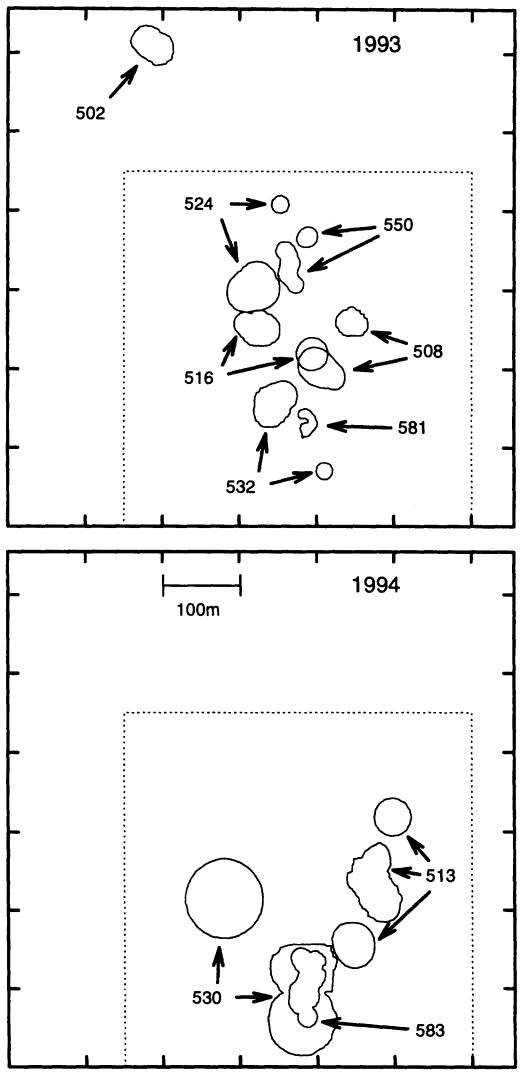

FIG. 1.—Home ranges of pygmy rabbits (*Brachylagus idahoensis*) monitored at Fossil Butte National Monument, Wyoming, during winters 1993 and 1994. Each number shows the core areas for an individual. Habitats within the dotted areas were sampled to characterize the general areas used by pygmy rabbits, whereas areas outside the box were sampled to represent available, but unused, habitats.

RESULTS

Sizes of home ranges used by pygmy rabbits were variable, with a maximum of a 33-fold difference between animals. Areas used by individuals averaged 2,568 ± 426 m^2 (range = 548–3,701 m^2; $n = 7$) in 1993, and 10,204 ± 4,415 m^2 (range = 3,372–18,464 m^2; $n = 3$) in 1994. Size of home ranges differed significantly between years ($t = 2.6$, $d.f. = 8$, $P = 0.03$), and was not dependent on number of telemetry locations ($r = 0.05$, $d.f. = 8$, $P = 0.45$). We detected two or more core areas within seven of the 10 home ranges (Fig. 1). Boundaries of ad-

jacent core areas were never >100 m apart, and frequently were separated by <50 m. Movement among core areas was variable, occurring as frequently as daily for some animals and only once for others. Pygmy rabbits used the same general areas in 1994 as in 1993, although none of the same individuals were monitored for consecutive years. Core areas tended to overlap between and within years, and several areas were used concurrently by three or more rabbits.

The general area inhabited by pygmy rabbits (Fig. 1) had significantly more shrubs, greater coverage of shrubs, and taller, wider shrubs than did adjacent areas where rabbits never were observed (Table 1). Even within home ranges, amount of cover and number, height, and size of canopies of sagebrush tended to be greatest in areas used most by pygmy rabbits. Heights of living and dead shrubs and minimum height and size of canopies of shrubs were the only variables strongly correlated ($r > 0.7$) with each other. Shrubs in areas of low use had a greater proportion of living branches than shrubs in other areas. Indeed, areas used with highest frequency by pygmy rabbits had a substantial component of dead shrubs. Height of the dead component in those areas was greater, as was number of dead shrubs per unit area, than in areas not used as extensively by the animals. Interestingly, percentage frequency of dead shrubs did not vary among areas of different use within home ranges, although the amount of dead material increased proportionately with intensity of use. Basin big sagebrush composed a much greater proportion of shrubs in areas of high use than in other areas. Density of Wyoming big sagebrush (*A. t. wyomingensis*), however, actually was greater in areas of medium use compared with areas of high, low, and no use.

Habitats generally used by pygmy rabbits, as well as core areas used most frequently within home ranges, had a significantly denser vegetative profile, except from 0 to 10 cm above the ground surface, than other sampled areas (Fig. 2). Areas with no or low use by rabbits had less coverage by canopies of shrubs and more low grasses, forbs, and alkali sagebrush (*A. longilobila*) resulting in a higher number of contacts near the ground.

Depths of snow were greater in areas used heavily by pygmy rabbits in 1993 than in areas that received little use ($F = 6.66$; $d.f. = 1, 6$; $P = 0.04$; Table 2). Average depths of snow ranged from 49 to 88 cm on transects in areas used most frequently, and from 33 to 82 cm on transects in areas used less frequently. Depth of snow remained constant during 1994, and averaged 16.3 ± 1.6 cm ($n = 7$) in areas of high use and 23.8 ± 4.3 cm ($n = 7$) in areas of low use. Differences in depth of snow between areas of high and low use in 1994 were not significant ($t = 1.65$, $d.f. = 7$, $P > 0.05$).

Vegetative structure above the snow's surface was variable and apparently related to depth of snow in 1993 (Table 3). Average height of shrubs, size of canopies, number of shrubs and percentage cover declined as depth of snow increased in all areas. The number of exposed shrubs was 2–3 times greater and percentage cover was 3–20 times greater in 1994 than in 1993.

Discussion

Home ranges of pygmy rabbits during winter on Fossil Butte were similar in size to those reported from previous studies. Others have suggested that pygmy rabbits rarely range >30–50 m from their burrows during winter (Bradfield, 1975; Jansen, 1946; Wilde, 1978). If we assume a circular home range, our data imply that movements averaged 13–53 m. Because burrows were not necessarily in the center of the home range and because most animals had more than one core area, we often observed movements of >100 m by rabbits. Gahr (1993) reported home ranges of 20.2 ha for males and 2.7 ha for females during summer in Washington, which were considerably larger than the sizes of home ranges we found. In Washington, some rabbits

TABLE 1.—*Habitat characteristics* ($\bar{X} \pm SE$) *measured on 50-m transects in areas used and not used by pygmy rabbits* (Brachylagus idahoensis) *and on 10-m transects in the core areas of home ranges of pygmy rabbits during the winters of 1993 and 1994 at Fossil Butte National Monument, Wyoming. Test statistics tested for differences between and among classes.*

	General area of use				Level of use within home ranges					
Variable	Not used (n = 8)	Used (n = 8)	F-statistic	P	No (n = 5)	Low (n = 46)	Medium (n = 38)	High (n = 35)	F-statistic	P
Number of live shrubs per meter	0.09 ± 0.03	1.25 ± 0.06	356.4	<0.001	0.28 ± 1.8	9.5 ± 0.8	11.3 ± 1.0	13.0 ± 0.8	6.8	<0.001
Number of dead shrubs per meter	0.008 ± 0.004	0.39 ± 0.04	83.6	<0.001	0.12 ± 0.8	2.8 ± 0.5	3.4 ± 0.4	4.9 ± 0.6	4.3	0.006
Number of *A. t. wyomingensis* per meter	0.06 ± 0.02	1.02 ± 0.07	169.7	<0.001	0.22 ± 1.4	6.7 ± 0.7	8.8 ± 1.0	6.8 ± 0.8	3.1	0.030
Number of *A. t. tridentata* per meter	0.03 ± 0.02	0.16 ± 0.06	4.4	0.055	0.06 ± 0.6	1.0 ± 0.3	1.5 ± 0.6	4.2 ± 0.6	7.9	<0.001
Percentage cover	16.5 ± 2.0	42.9 ± 3.0	53.7	<0.001	25.9 ± 8.7	38.6 ± 1.9	42.7 ± 2.3	51.1 ± 2.1	8.4	<0.001
Percentage alive	51.6 ± 12.0	45.0 ± 2.6	0.3	0.595	26.3 ± 16.1	48.6 ± 1.7	40.7 ± 2.2	37.2 ± 1.5	0.1	<0.001
Maximum living height of shrubs (cm)	27.6 ± 7.0	55.2 ± 3.7	12.2	0.004	18.9 ± 11.8	48.4 ± 2.2	57.9 ± 2.7	75.3 ± 3.3	24.9	<0.001
Maximum height of dead shrubs (cm)	21.1 ± 5.9	48.1 ± 2.9	16.8	0.001	13.4 ± 8.4	40.9 ± 1.8	51.5 ± 2.5	67.7 ± 3.5	27.3	<0.001
Minimum living height of shrubs (cm)	5.4 ± 1.6	18.1 ± 1.9	26.4	<0.001	2.7 ± 1.7	13.7 ± 1.1	19.1 ± 1.4	29.5 ± 2.1	24.9	<0.001
Size of canopy (cm)	25.9 ± 6.7	51.9 ± 2.6	13.3	0.003	22.4 ± 13.9	49.8 ± 2.2	55.6 ± 2.7	60.7 ± 2.4	9.6	<0.001

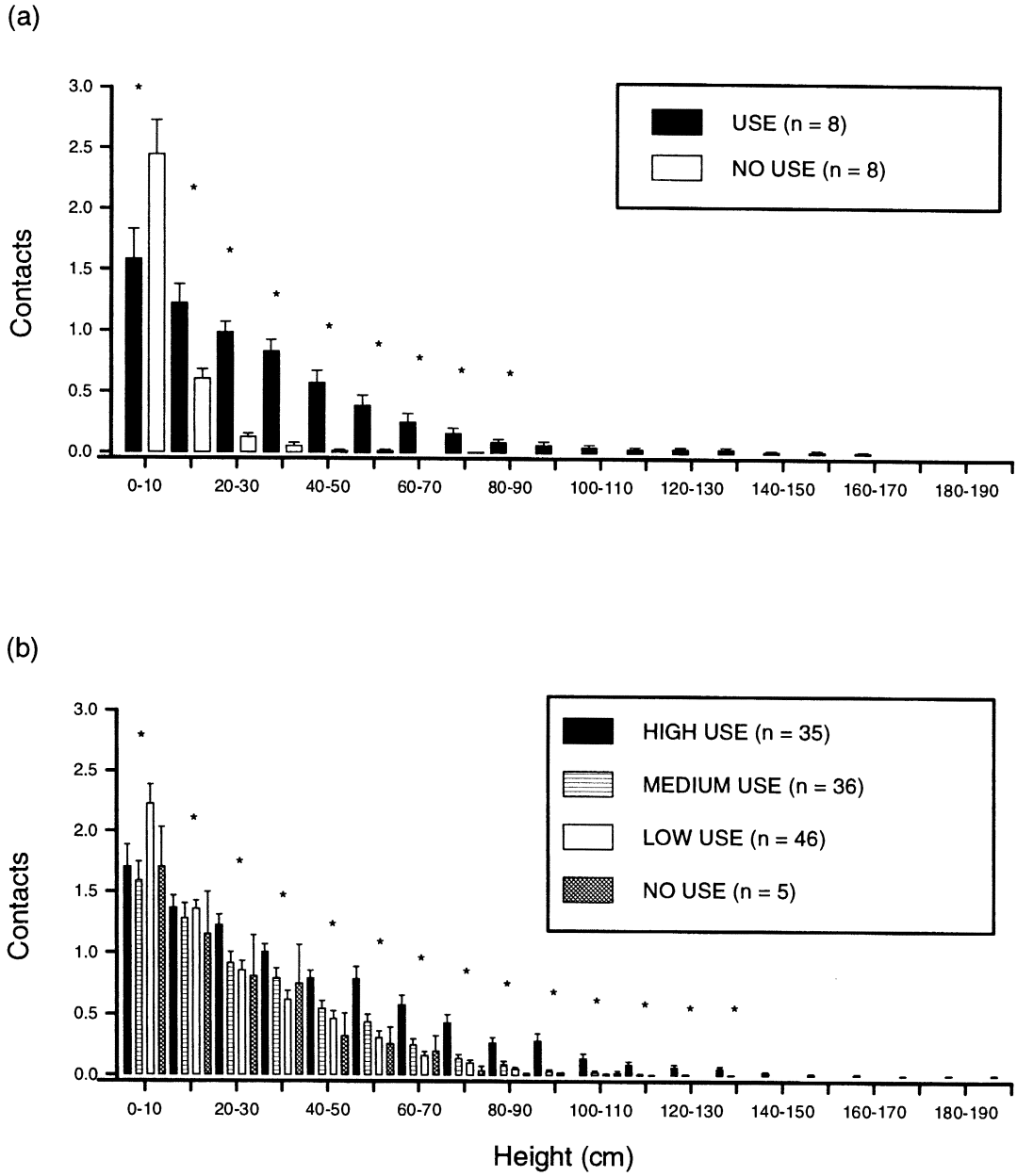

FIG. 2.—Comparison of vegetative profile for a), areas used and not used by pygmy rabbits (*Brachylagus idahoensis*) and b), for differential use of areas within home ranges of pygmy rabbits at Fossil Butte National Monument, Wyoming, during winters 1993 and 1994. An asterisk indicated significant differences between and among groups at $P < 0.05$.

lived in grazed habitats where they may have had to travel farther to find suitable patches of habitat. Additionally, this work was done during the breeding season, which particularly influenced movements of males (Gahr, 1993). We were unable to analyze differences in home ranges between sexes because of limited sample size and extreme

TABLE 2.—*Average depth of snow in cm;* ($\bar{X}$ ± SE) *in areas used with high* (n = 4) *and low* (n = 4) *frequency by pygmy rabbits* (Brachylagus idahoensis) *at Fossil Butte National Monument, Wyoming, in January, February, and March 1993. Comparisons between groups of high and low use on each date were significantly different* ($P \leq 0.05$) *except for 20 January.*

Date	Use	
	High	Low
12 January	57.2 ± 1.6	43.6 ± 5.8
20 January	51.1 ± 1.0	45.9 ± 4.7
28 January	56.2 ± 0.2	42.7 ± 5.1
5 February	54.3 ± 0.4	43.6 ± 4.5
15 February	56.6 ± 0.4	45.8 ± 4.7
24 February	83.2 ± 1.7	56.1 ± 9.1
1 March	79.6 ± 1.9	51.4 ± 8.6

differences between years, which resulted from different patterns of snowfall.

We believe that the greatest influence on size and structure of home ranges was the difference in amounts of snow in 1993 and 1994. The tendency for home ranges at Fossil Butte to have more than one core area likely was related to the patchy nature of the habitat, which was further intensified by snowfall. In 1993, vegetative structure provided by clumps of sagebrush acted as a snow fence, trapping blowing snow in areas the rabbits used. Consequently, depths of snow in those areas ranged from 40 to 120 cm. Use of habitat above the snow's surface in 1993 was restricted to small patches of tall *A. t. tridentata* that often were separated by large snowfields with no visible vegetation. In 1994, depths of snow ranged from 0 to 35 cm in the same areas, and considerably more cover occurred between patches of sagebrush. The tallest patches were used in both years, but home ranges in 1994 also extended into adjacent areas that were under snow the previous year. Use of those areas as corridors for movement and sites for foraging likely accounted for the larger home ranges observed in 1994.

McNab (1963) suggested that size of a home range increases as resources decrease in availability. Pygmy rabbits in our study appeared to decrease the size of their home ranges as total exposed food and vegetative cover became less available to them. Creation of extensive systems of subnivean burrows, however, provided access to persistent sagebrush under the snow, making it unlikely that food was limiting. The subnivean environment compensated for the apparent loss of available habitat at the snow's surface and provided rabbits with a constant, nutritious source of food (Behan and Welch, 1986). Pygmy rabbits consume all three subspecies of big sagebrush (*A. t. tridentata, A. t. wyomingensis,* and *A. t. vaseyana*). We suggest that amount of vege-

TABLE 3.—*Vegetative characteristics* ($\bar{X}$ ± SE) *of snow-covered 20-m transects in areas of high and low use by pygmy rabbits* (Brachylagus idahoensis) *at Fossil Butte National Monument, Wyoming. Sampling was conducted in mid-January* (n = 4) *and late February* (n = 4) *in 1993 and late January* (n = 7) *in 1994.*

Level of use	Number of shrubs per meter	Percentage cover	Height of shrubs (cm)	Size of canopy (cm)
Mid-January 1993				
High	0.6 ± 0.1	5.8 ± 1.9	48.5 ± 8.6	66.3 ± 7.5
Low	0.3 ± 0.2	2.2 ± 1.9	29.5 ± 3.3	57.9 ± 2.1
Late-February 1993				
High	0.4 ± 0.1	0.8 ± 0.4	33.1 ± 9.3	44.1 ± 13.6
Low	0.2 ± 0.1	0.6 ± 0.4	18.3 ± 2.1	41.0 ± 5.4
Late-January 1994				
High	1.3 ± 0.1	18.8 ± 3.5	65.7 ± 10.8	65.3 ± 4.7
Low	0.7 ± 0.1	6.8 ± 1.7	44.9 ± 5.6	49.6 ± 3.5

tative cover above the snow is the primary determinant of size of core areas used by pygmy rabbits during winter at Fossil Butte. Cover by shrubs is an important component of habitat for snowshoe hares (*Lepus americanus*) and eastern cottontails (*Sylvilagus floridanus*—Ferron and Ouellet, 1992; Keith and Bloomer, 1993) and may provide protection from predators (Small and Keith, 1992). As cover of shrubs decreases, vegetative corridors connecting clumps of tall plants are eliminated. Movement by rabbits between patches becomes more visible to predators, and, therefore, movements are expected to occur less frequently (Keith et al., 1993).

The general areas used at a large scale by pygmy rabbits were characterized by evenly distributed, tall, big sagebrush with dense canopies. Those areas tended to have two or more subspecies of sagebrush and few forbs (Katzner, 1994). Adjacent, unused areas typically had fewer, shorter, and younger shrubs in well-spaced, monotypic clumps than in used areas. The percentage cover and height of sagebrush in habitats used by rabbits at Fossil Butte were similar to cover and height of shrubs used during summer on a similar scale (Green and Flinders, 1980*a*). The consistency between habitats used by pygmy rabbits in Idaho and Wyoming implies that amount and structure of cover are as critical to pygmy rabbits as they are to rabbits in other ecosystems (Gibb, 1993; Kolb, 1994; MacCracken et al., 1988; Small and Keith, 1992; Swihart and Yanher, 1984; Trent and Rongstad, 1974).

At a smaller scale within the core areas used by pygmy rabbits, use was related directly to vertical density and diversity of habitat. Areas of highest use, characterized by *A. t. tridentata,* had taller, more dense biomass of shrubs, more standing dead vegetation, and a thick canopy covering a large proportion of the area. Areas of medium use, characterized by *A. t. wyomingensis,* tended to occur adjacent to areas of high use. Wyoming big sagebrush is a shorter, less structurally diverse shrub typically found in slightly drier areas than *A. t. tridentata.* Severaid (1950) also observed that pygmy rabbits preferred areas with the most dense sagebrush, and other studies have noted the relationship between height of shrubs, percentage cover, and use by pygmy rabbits (Green and Flinders, 1980*a*; Weiss and Verts, 1984). Thickness of vegetative understory was correlated with densities and survival of European wild rabbits (*Oryctolagus cuniculus*), snowshoe hares, and cottontails (Ferron and Ouellet, 1992; Kolb, 1994; MacCracken et al., 1988; Swihart and Yahner, 1984; Trent and Rongstad, 1974). Raptors were the most significant source of mortality in our study and dense layers of vegetation likely would deter some birds and impede mammalian predators.

The amount of dead shrubs and twigs in habitats selected by pygmy rabbits has not been addressed in other studies. Because much of the living component of shrubs is higher above ground than is the dead component (minimum living height in high use areas = 29.5 cm; minimum dead height in all areas averaged 0 to 5 cm), the dead layer provides structure at lower heights. It is unknown whether this dead layer is simply a natural consequence of aging stands of sagebrush or if pygmy rabbits actually contribute to its formation. Nonetheless, the non-living structure of twigs and shrubs may further contribute to protection from predators and maintenance of subnivean sites for burrowing.

In addition to vegetative characteristics of areas used most frequently by pygmy rabbits, specific soil types for burrowing may be important, as found for European wild rabbits (Parer and Libke, 1985). Those areas that support the densest stands of basin big sagebrush at Fossil Butte have deep loamy soils (Shumar and Anderson, 1986), which are easy to excavate. In Washington, pygmy rabbits are known to use certain soil types so exclusively that previously unknown populations were located by looking

in areas with these specific characteristics of soils and shrubs (J. T. Kehne, in litt.)

The apparent dependence on a dense understory, provided partially by dead shrubs and extensive canopies, may explain the decline in populations of pygmy rabbits over most of the grazed habitats of the sagebrush-steppe in the western United States. Land that is grazed intensively by domestic herbivores often has relatively low structural complexity and may not adequately support populations of pygmy rabbits (Holecheck, 1981; Wilde, 1978). Fragmentation of habitats also can influence size, stability, and success of those populations because of the low capabilities for dispersal by pygmy rabbits and an apparent reluctance to cross open habitat (Dobler and Dixon, 1990; Green and Flinders, 1980*a*; Weiss and Verts, 1984). Our data suggest that pygmy rabbits may be influenced negatively by the destruction of dense, structurally diverse patches of sagebrush and corridors that connect them. Future studies should compare selection of habitat by pygmy rabbits in grazed or younger stands of sagebrush with selection of habitat in older stands to further define the importance of structure and diversity of vegetation to survival of the pygmy rabbit.

Acknowledgments

The National Geographic Society, the University of Wyoming, the University of Wyoming National Park Service Office, and Fossil Butte National Monument provided funding for this project. We are indebted to A. Stikkel, P. Battles, S. Peterson, and the staff at Fossil Butte National Monument for their assistance in the field. M. P. Gillingham, S. W. Buskirk, D. H. Knight, and G. Hayward provided statistical and methodological advice and made helpful suggestions on the manuscript.

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Submitted 23 December 1994. Accepted 16 December 1996.

Associate Editor was Glennis A. Kaufman.