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DEN CHARACTERISTICS AND SURVIVORSHIP OF WOODRATS (*NEOTOMA LEPIDA*) IN THE EASTERN MOJAVE DESERT

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ABSTRACT—A population of desert woodrats (*Neotoma lepida*) in the eastern Mojave desert was studied for a period of three years. All 101 dens located within a 2.7 ha plot were identified, and trapped on a roughly bimonthly schedule. Den occupancy rates (occupied dens/dens trapped) fell from a high of almost 50% at the initiation of the study to a level of approximately 5–10% due to the effects of a severe drought. Body mass of individuals remained roughly constant during this period, however, suggesting that mortality was not due to starvation. Mean survival on the site was 5.4 months, with no significant difference between the sexes. Several characteristics of the den appeared to influence survivorship, including the primary structural material and overall size. Occupancy and survivorship rates were significantly higher in *Opuntia* than in other substrates, presumably because of increased predator protection. Reproductive output was strongly curtailed during most of the study. Woodrats reproduced only once in 1988, and not at all in 1989. The reproductive failure coincided with a lack of annual plant production and seed set by perennials such as *Yucca schidigera*.

Burrows and dens play an important role in many ecological aspects of an animal's existence. They may provide a more favorable habitat by modifying the physical environment, increasing protection from predators, facilitating social interactions between conspecifics, or through some combination of these factors (McNab, 1966; Brown, 1968; Nevo, 1979; Hansell, 1984, 1987, 1993; Meadows, 1991; Neal and Roper, 1991). While a variety of desert animals actively construct houses or burrows, woodrats (*Neotoma*) are particularly well known for their large conspicuous dens. Generally these are complex conical structures with a variety of entrances and internal chambers, and can in some woodrat species exceed 2 m in both basal diameter and height (Vorhies and Taylor, 1940; Linsdale and Tevis, 1951; Fitch and Rainey, 1956; Stones and Hayward, 1968; Bonaccorso and Brown, 1972; Cameron and Rainey, 1972; Olsen, 1973; Wright, 1973). The vast majority of the structure is above ground, although some dens may contain subterranean passages depending on the species and soil substrate (Linsdale and Tevis, 1951). Studies on den site selection have suggested that thermal considerations, proximity to food sources, and predator deterrence are all important factors determining the choice of woodrat den location (e.g., Monson and Kessler, 1940; Vorhies and Taylor, 1940; Fitch and Rainey, 1956; Brown, 1968; Cameron and Rainey, 1972; Olsen, 1973; Wright, 1973; Turkowski and Watkins, 1976; Cranford, 1977; Vaughan and Czaplekski, 1985).

As part of a study examining the trade-offs between nutritional strategy and life history attributes in small herbivores (Justice and Smith, 1992; Smith, 1992; Smith, 1995), a population of desert woodrats (*Neotoma lepida*) in the eastern Mojave desert was monitored for three years. The study coincided with the onset of a drought in California. During this period of severe environmental conditions, less than half the average precipitation fell and many annual plants failed to appear (Fig. 1). I attempted to quantify the relationship between woodrat survival and the type of den inhabited; to determine if survivorship was influenced by the type of den occupied; and to determine the caused of woodrat mortality.

MATERIALS AND METHODS—The study was conducted at the University of California Granite Mountain Reserve (UCGMR), located approximately 130

km east of Barstow, San Bernardino County, California, in the eastern Mojave Desert (24°47′N, 115°43′W). It is situated in a transition zone containing floral and faunal elements of the Great Basin, Sonoran, and Mojave deserts. The climate is intermediate between these regions, with a slightly skewed bimodal rainfall pattern. Mean annual precipitation is 18.6 cm, and typically occurs in both late summer and winter, with the majority during the latter period (Stein and Warrick, 1979). The Cove Springs study site (ca. 2.7 ha) is located at the base of the Granite Mountains at 1200 m elevation within a *Yucca-Opuntia-Coleogyne* scrub community. The diverse vertebrate fauna includes 13 sympatric rodents as well as 33 reptilian and 115 avian species (Johnson et al., 1979). Here I use the terms *house* and *den* interchangeably; some authors have restricted the use of *den* to structures located within rocky outcrops (e.g., Olsen, 1973).

Plot sampling was conducted during fall and spring of 1989–1990 to measure vegetation abundance on the site. This permitted computation of expected den frequencies based on vegetation type. Rectangular plots with an area of 10 m^2 have been reported to yield accurate results when the average height of vegetation ranges from 2 to 4 m (Brower and Zar, 1984), as it does at UCGMR. Accordingly, ten 10 m^2 plots were sampled during each period, with both location and orientation selected randomly. Vegetation was identified to species and width, length and height were measured, permitting calculation of percent cover and biomass for each plant type. Temperature and precipitation data were obtained from a weather station located on the reserve approximately 2 km from the study site.

The precise location of all dens within the main study area was established using aerial photographs and calibrated with standard surveying techniques. The plant constituting the primary structural support was identified. Measurements were taken of den width, length and height, and volume was estimated assuming a rectangular geometry. Because dens are actually rounded or conical (e.g., Cameron and Rainey, 1972), this measure systematically overestimated absolute above-ground mass. There was no relationship between den shape and structural material, however, so a rectangular volume estimate provided an adequate relative measure. No estimation was possible of subsurface volume because dens were not destructively sampled. This probably did not greatly affect volume estimates because woodrats generally do not excavate extensive subterranean burrows (e.g., Vorhies and Taylor, 1940).

All dens were trapped for a period of 1–4 days on a roughly bimonthly schedule. Two Sherman live-traps were placed at each den location to minimize underestimation of occupancy rates caused by capture of other rodents. Both apple slices and grain were used as bait, and several cotton balls were added for insulation. Beginning in early 1989, all traps were enclosed within cardboard milk cartons. These served as insulators against temperature extremes and eliminated fatalities due to exposure during inclement weather. Upon initial capture, woodrats were uniquely identified by attaching a numbered fingerling tag to each ear. During each subsequent capture, animals were weighed, sexed, and reproductive condition was assessed.

To determine if the type of den occupied influenced woodrat survivorship, woodrats were scored as to the den type they most frequently inhabited, and survivorship was calculated. In most instances this was relatively straightforward, since in this habitat woodrats tend to exhibit high fidelity to a single den location. The several animals for which a preference could not be determined were excluded from the analysis. To distinguish between the causes of woodrat mortality within the population, I examined the difference in body mass between the last two captures for adult animals that disappeared during the course of the study. I expected that if inadequate food, water or disease were the fundamental cause(s) of woodrat mortality, body mass would decrease during this interval. Body mass trends were also investigated for the entire study period by conducting regressions on the nine adult animals for which three or more capture records existed.

RESULTS—Total plant cover at the Cove Springs study site is approximately 38%, with the most prevalent species consisting of blackbrush (*Coleogyne ramosissima,* 26.5% of all plants present), Mojave yucca (*Yucca schidigera,* 14.5%), and buckhorn cholla (*Opuntia acanthocarpa,* 7.2%). Although blackbrush is numerically the most abundant, Mojave yucca is the dominant species in terms of percent plant cover (35% versus 15.5%). Plant species present in very low numbers were not sampled. Annual rainfall was sharply curtailed during both 1988 and 1989 (Fig. 1).

During the study, 54 woodrats were captured and tagged. Of these, 21 were caught more than twice. The mean survival time for animals captured two or more times was 5.4 months (Table 1); this value was only 3.3 months if all animals were considered. Differences in survivorship were not statistically distinguishable between the sexes (Mann-Whitney U-test, $P > 0.05$). Differences in juvenile versus adult survival were not tested because sample sizes were too small to further subdivide. There was, however, a much higher tendency on the part of juvenile females to be caught during the next trapping interval (ca. 67%) than for juvenile males (ca. 30%), presumably reflecting greater natal site dispersal on the part

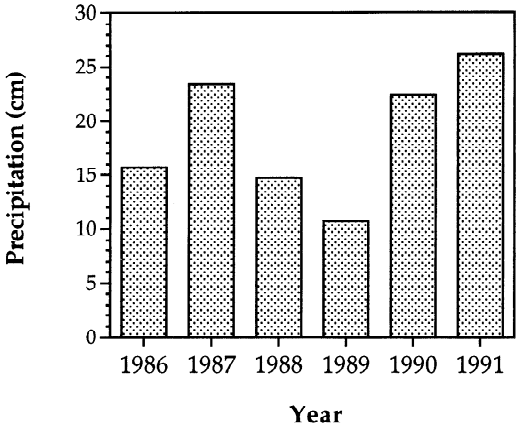

FIG. 1—Annual precipitation (in cm) for 1986 to 1991 at the UC Granite Mountain Reserve. Annual precipitation averages about 19 cm, based on 50 years of records. The study was begun in spring of 1988 and continued until spring of 1991.

of males. Woodrats either maintained or gained body mass shortly before their disappearance from the study site (Wilcoxon's one-tailed signed-rank, $P > 0.05$, $d.f. = 14$). On average, adult woodrats gained approximately 2% of body mass between the last two captures (Table 1), with no difference evident between the sexes. Reproductive status did not seem to influence survivorship; only two of the 15 animals were sexually reproductive when last captured. Slopes of the regressions of body mass for seven of the nine adults captured multiple times were either zero or positive, also indicating that woodrats were maintaining or gaining body mass during the course of the study. No woodrats were captured in reproductive condition from August 1988 until March 1990.

TABLE 1—Survival and mass change among woodrats at Cove Springs, UCGMR. Survival estimate excludes animals still alive at end of study; percent mass change also excludes juvenile animals. Differences between the sexes are not statistically significant.

	Survival (months)			% mass change during last capture interval		
	n	$\bar{X}$	$\pm SD$	n	$\bar{X}$	$\pm SD$
Males	7	6.9	±5.44	5	2.04	±5.77
Females	11	4.6	±3.39	9	1.32	±6.95
Overall	18	5.4	±4.45	14	1.58	±6.56

Houses were constructed exclusively around three types of plants: Mojave yucca, buckhorn cholla, and to a far lesser extent, pencil cholla (*Opuntia ramosissima*; Table 2). Three dens constructed of both Mojave yucca and buckhorn cholla could not be assigned unambiguously to either category, and were excluded from all analyses. Although there was a highly significant preference for both yucca and cholla to be utilized over other plant types (G-test, $P < 0.001$, $d.f. = 2$), woodrats appeared to be evenly distributed among both cholla and yucca dens (G-test, $P > 0.05$, $d.f. = 1$). When corrected for the greater number of yucca dens available, however, it became apparent that cholla dens were preferentially inhabited (G-test, $P < 0.05$, $d.f. = 1$). The average volume was significantly larger for cholla dens than other types (Table 2; two-tailed t-test, $P < 0.05$, $d.f. = 94$); probably reflecting the higher occupancy rate and hence longer construction and maintenance period.

When the study was initiated in the spring of 1988 the den occupancy rate was high (ca. 50%; Fig. 2). It subsequently declined to 5–10% and remained roughly constant at this level for close to a year before dropping to zero in the winter of 1990. Den occupancy rate is used here rather than a population density estimate because the study site was expanded substantially during 1989, and because woodrats are nonrandomly distributed across the habitat. Thus, neither the area of the study site nor trapping effort were uniform.

Considerable variation existed in the frequency in which woodrat dens were occupied (Fig. 3), although those in cholla were generally occupied for longer periods than those in yucca (two-tailed t-test, $P < 0.001$, $d.f. = 94$; Fig. 4). Most dens were rarely, if ever, inhabited during the course of the study, while others were more or less continually occupied by a succession of woodrats. Approximately 62% of the time, animals were captured at the same den location (referred to here as the primary den). Males used significantly more ancillary dens than did females (3.83 ± 1.77 versus 2.13 ± 1.25; two-tailed t-test, $P < 0.05$, $d.f. = 18$), although there was no difference between the sexes in the proportion of time spent at the primary den (62% vs. 63%). At no time was more than one adult woodrat caught at a den; plural occupancy of houses is limited to females with young (e.g., Monson and Kessler, 1940;

TABLE 2—Characteristics of woodrat dens at Cove Springs, UCGMR. Dens were constructed only around these three plant types. CI = 95% confidence interval.

Den structural support	No. of dens	Relative abundance of plant (%)	% dens built in plant	Den size (m^3)		Occupancy rate (%)	
				Mean	±CI	Mean	±CI
Mojave Yucca	61	14.5	63.5	0.40	0.086	7	2.3
Buckhorn Cholla	35	7.2	34.4	0.54	0.122	13	4.7
Pencil Cholla	2	3.0	2.1	0.35	—	13	—

Vorhies and Taylor, 1940; Linsdale and Tevis, 1951; Fitch and Rainey, 1956; Stones and Hayward, 1968; Turkowski and Watkins, 1976).

Mean survival was higher for animals inhabiting dens in cholla (4.1 months ±1.8) than it was for those found in yucca (2.5 months ±1.4; Fig. 4). This difference was significant (one-tailed t-test, $P < 0.05$, $d.f. = 43$) and was not affected by gender.

DISCUSSION—The high den occupancy rate (ca. 50%) observed at the beginning of the study is probably a result of the heavy precipitation of the previous year (Fig. 1). Not only was there greater than average precipitation in 1987, but the timing of rainfall (August to November) resulted in a tremendous burst in primary productivity during the late summer and fall of 1987 and during spring of 1988. Effects of the drought on vegetation were first evident during the spring of 1989, and were particularly severe that summer and the succeeding spring.

Drought conditions resulted in complete reproductive failure of the woodrat population during 1989. From August 1988 until March 1990, no woodrats were captured in reproductive condition and no juveniles were present on the study site. Mean survival from date of first capture was less than six months, suggesting that the majority of woodrats did not live long enough to reproduce. Lack of recruitment coupled with "normal" mortality resulted in a rapid decline and near extinction of the Cove Spring population. After a rapid initial decline, however, population density appeared to decrease very slowly, suggesting that mortality rates were relatively constant and were

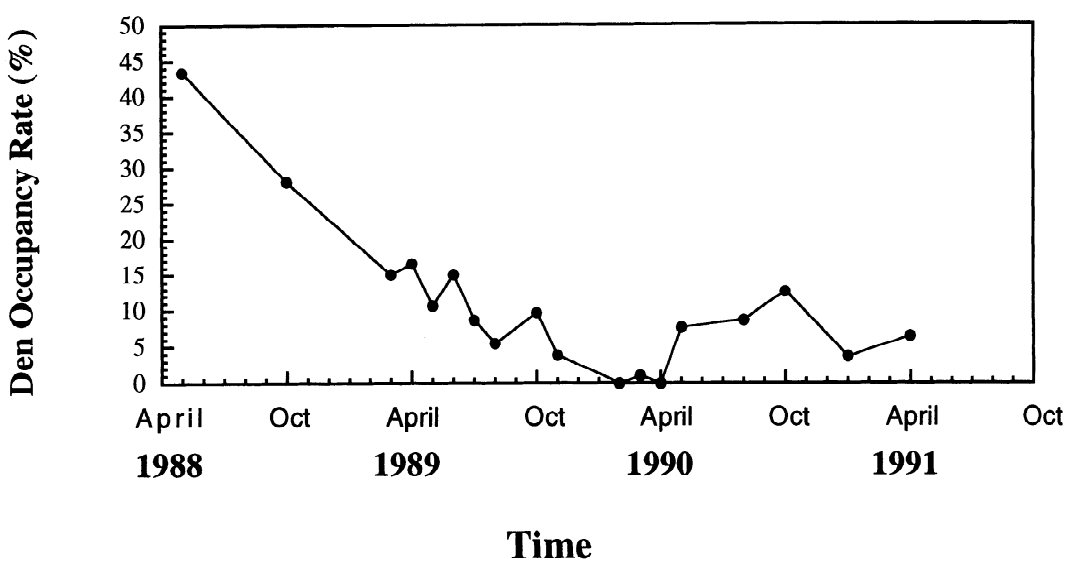

FIG. 2—Den occupancy rate during the study. Inclement weather during January and February of 1990 resulted in no captures, although animals were present.

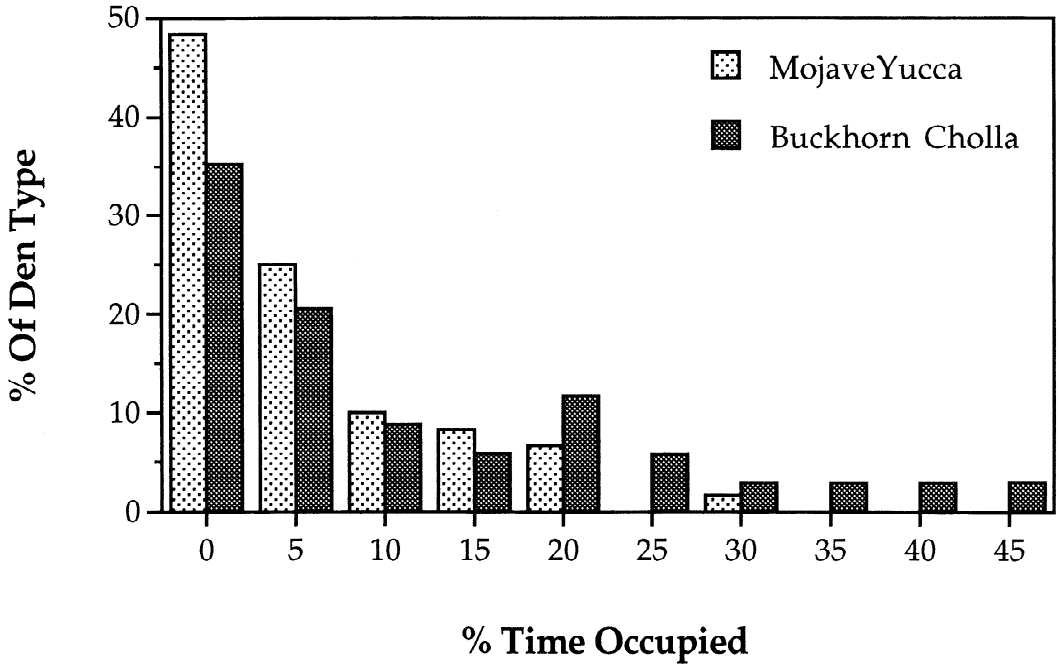

FIG. 3—Proportion of each den type versus occupancy rate. Approximately 47% of yucca dens and 35% of cholla dens were never occupied during the four years of the study.

not increasing during the period. Consistent with this pattern, the drought and subsequent decrease in primary productivity probably did not result in higher mortality due to starvation or water stress. The body mass of most animals remained constant or even increased slightly during the study period. Thus, it appears that adult woodrats were able to obtain sufficient food and water to survive, but lacked sufficient resources to reproduce. At the same time, the disappearance of woodrats from the study site was more likely due to mortality than emigration. Once mature, woodrats are relatively sedentary and are unlikely to disperse to new habitats (Vorhies and Taylor, 1940; Linsdale and Tevis, 1951; Raun, 1966). New adult animals were rarely captured during the four years of the study, and when new captures did occur, they were always located on the periphery of the study site.

If the majority of woodrat mortality was not a result of starvation, the most likely cause is predation. An obvious distinction between cholla and yucca dens is in the protection from predators they potentially provide. Cholla dens were primarily composed of a dense mat of intertwined cholla joints, offering substantial protection from all but the most persistent predators. Yucca dens, however, were mostly constructed from yucca leaves, which are relatively smooth along their margins although they have a particularly sharp tip. Despite the common name of "Spanish bayonet," dens composed of yucca leaves are probably considerably less of a deterrent to predators than those of cholla. It was interesting that although cholla joints were often seen on top of yucca dens, the reverse was rarely if ever observed. Numerous authors have noted that woodrats demonstrate strong preferences for certain plant types (e.g., Monson and Kessler, 1940; Vorhies and Taylor, 1940; Linsdale and Tevis, 1951; Fitch and Rainey, 1956; Stones and Hayward, 1968; Bonaccorso and Brown, 1972; Cameron and Rainey, 1972; Olsen, 1973; Wright, 1973; Turkowski and Watkins, 1976; Cranford, 1977; Vaughan and Czaplewski, 1985). Vorhies and Taylor (1940) noted that white-throated woodrats were often found under cacti. They went so far as to call such dens a "veritable fortress," and felt that only snakes could effectively gain access to animals housed within them (see also Cameron and Rainey, 1972). In Cove Springs, as in most other habitats, the majority of predation probably oc-

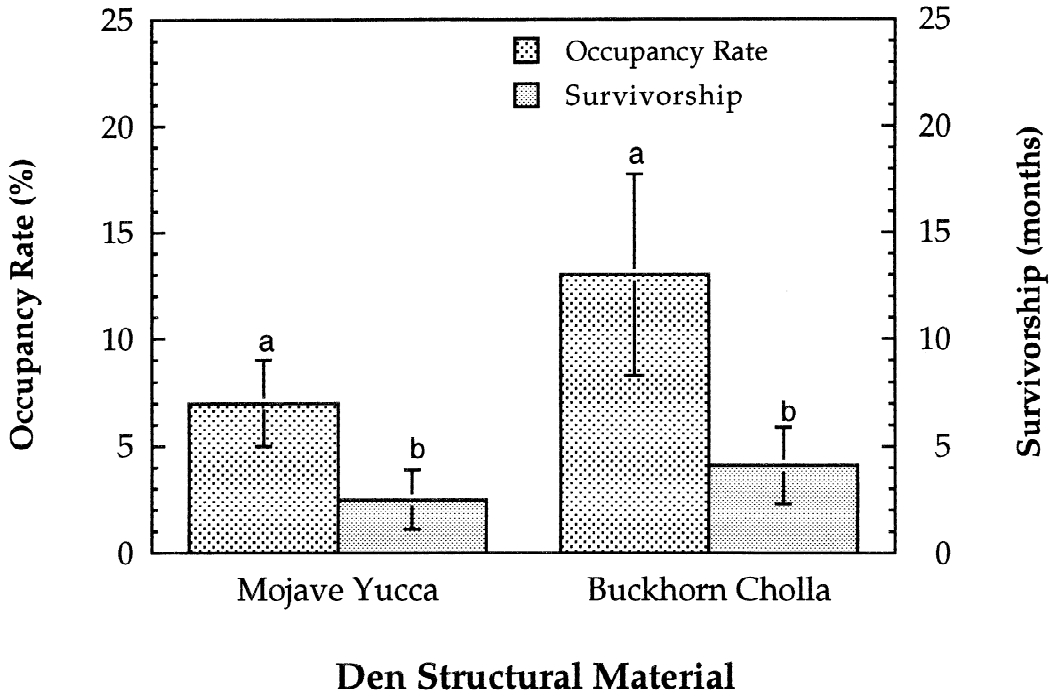

FIG. 4—Mean occupancy rate and woodrat survivorship (in months) for yucca and cholla dens. Both occupancy rates and woodrat survivorship differ significantly with the type of plant used as the main structural component. Bars with the same letter indicate significance at the $P < 0.05$ level.

curs while the animals are foraging. The most prominent predators were probably owls, and to a lesser degree, snakes. Over the course of the four year study, owls were heard or observed during virtually every trapping session. Evidence of coyotes, badgers, skunks and ringtails was occasionally seen, but much less frequently.

In general, the population cycle of woodrats at the Granite Mountains can best be described as "source/sink" dynamics (Pulliam, 1988; Pulliam and Danielson 1991). The bajada area in which the main study site was located represents a sink that is occupied during reasonable to good environmental conditions (e.g., during early 1988 and 1991). After woodrat density dropped to nearly zero in 1990, extensive line trapping was conducted in a roughly 20 ha area around the study site. The only animals caught were those situated in rocky outcrops adjacent to the study area. Survivorship was apparently higher in this particular rocky area, perhaps due to the additional protection afforded by the complex nature of the dens. Other authors have noted that rocky outcrops provide better predator protection than other types of dens, and have suggested that woodrats occupy them preferentially (e.g., Fitch and Rainey, 1956; Brown, 1968; Cameron and Rainey, 1972; Olsen, 1973). Recruitment into the original Cove Springs population occurred in spring and summer of 1990 (Fig. 2), when juveniles were again found on the site. Trapping of the adults in the rocky outcrop during the same time period revealed that all were in reproductive condition. Thus, it appears likely that these individuals were responsible for recolonization of the main study area.

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