ECOLOGICAL DISTRIBUTION OF WOODRATS

IN

GUADALUPE MOUNTAINS NATIONAL PARK, TEXAS

by

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IN

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INTRODUCTION

The preservation of our national parks for enjoyment and enlightenment of future generations depends on maintenance of human impact at levels which will not degrade natural assemblages of plants and animals. The slogan of the National Park Service, "parks are for the people," challenges us to develop management plans that will permit maximum use of the parks with minimal impact on the local ecosystems. A thorough understanding of interrelationships and ecological requirements of a park's flora and fauna is a prerequisite to solving this difficult problem. Once these relationships are known, methods of measuring human impact on the ecosystem must be developed and employed to monitor the condition of the ecosystem.

Although small mammals are an important part of the ecosystem, they have generally been overlooked in the development of resource management plans. Small mammal studies in our national parks have tended to be descriptive inventories without management implications. Some of the small mammalian species occurring in our national parks are endangered and should be actively managed to enhance their chances of survival. Small mammals also deserve careful study because of their role as prey for carnivores, because they may compete with other animals for food resources, and because of their impact, both positive and negative, on the flora of a park. A final consideration is utilization of small mammals as biological indicators of habitat conditions within a park.

Biological indicators are organisms, species, or communities which indicate the presence of certain environmental conditions. Plants have been widely used as indicators of habitat conditions and have proved useful as habitat management aids. Animals associated with these plants can also be utilized as habitat indicators. Human impact in a national park can be determined in part by monitoring changes in quantity and quality of different types of habitats and accompanying changes in density and distribution of associated animals.

The purpose of this research was to determine the distribution of woodrats in Guadalupe Mountains National Park, to quantify the size and components of representative woodrat houses, to analyze the habitat in the immediate vicinity of these houses, and to investigate the feasibility of using woodrats as biological indicators of habitat conditions.

Three species of woodrats occur in Guadalupe Mountains National Park. In 1901, Bailey (1905) collected *Neotoma albigula* in Dog Canyon. He also reported that *Neotoma mexicana* was common at higher elevations in the Guadalupe Mountains of Texas, living in rocks and cliffs and ranging to the tops of the mountains. Davis (1940) trapped one *Neotoma albigula* at Frijole in 1938 and one *Neotoma mexicana* in a log cabin in The Bowl in 1939. Davis and Robertson (1944) reported *Neotoma micropus* from Culberson County, Texas, but did not indicate their presence in the immediate vicinity of the Guadalupe Mountains. All three species of woodrats were captured within the boundaries of Guadalupe Mountains National Park during my initial mammal survey work in 1973.

METHODS AND MATERIALS

The distribution of woodrats in Guadalupe Mountains National Park was mapped as the result of extensive trapping throughout the park in conjunction with a survey of mammals of the park. Woodrats were captured in sherman folding aluminum live traps, wire-mesh traps (18 X 4½ X 5 inches), and Victor rat traps. Several woodrats were shot with a .22 caliber pistol. Specimens were deposited in The Museum, Texas Tech University. Most specimens were standard museum skins and skulls, with some skulls without skins, complete skeletons without skins, and skulls accompanied by bodies preserved in alcohol. For descriptions and locations of collecting sites and accounts of species, see Genoways *et al*. (1975). Usages of the terms "house," "den," and "nest" follow Finley (1958). A "den" is any large outer shelter enclosing the living area of the occupant, a "house" is a den constructed by the occupant, and a "nest" is a small resting place lined with soft fibrous material.

Ten houses of *Neotoma albigula* and ten of *N. micropus* were examined. Individuals of *N. mexicana* do not construct houses and were, therefore, excluded from this phase of the study. Only houses from which the resident woodrat had been collected were selected for analysis. House length was measured at the longest point, width at the widest point perpendicular to the length, and height was measured at the highest point. Each house was dismantled. Materials used to construct the house were separated and weighed in a canvas sling suspended from a Chatillon spring-balance (calibrated from 0-15 kilograms). All materials of insufficient combined weight to be measured and all items apparently cached in a house were listed. Lengths, widths, heights, and weight of construction materials were analyzed by a one-way analysis of variance to test for significant differences among or between means (Sokal and Rohlf, 1969). When means were significantly different, the Student-Newman-Keuls (SNK) procedure was used to determine maximal nonsignificant subsets (Sokal and Rohlf, 1969).

The vegetation around each house and around ten den sites of *Neotoma mexicana* was sampled by means of a line-intercept method modified from the procedure described by Canfield (1941). Using the nest chamber as the midpoint, two 10 meter line-intercepts were established. One intercept was oriented north and south by compass and the other was oriented east and west (Fig. 1). A list of all plant species which occurred within the plot formed by connecting the ends of line-intercepts was recorded. From these lists floral similarity indices were computed for paired comparisons between plots. The indices were computed using the formula for Pirlot's index (Mosimann, 1968).

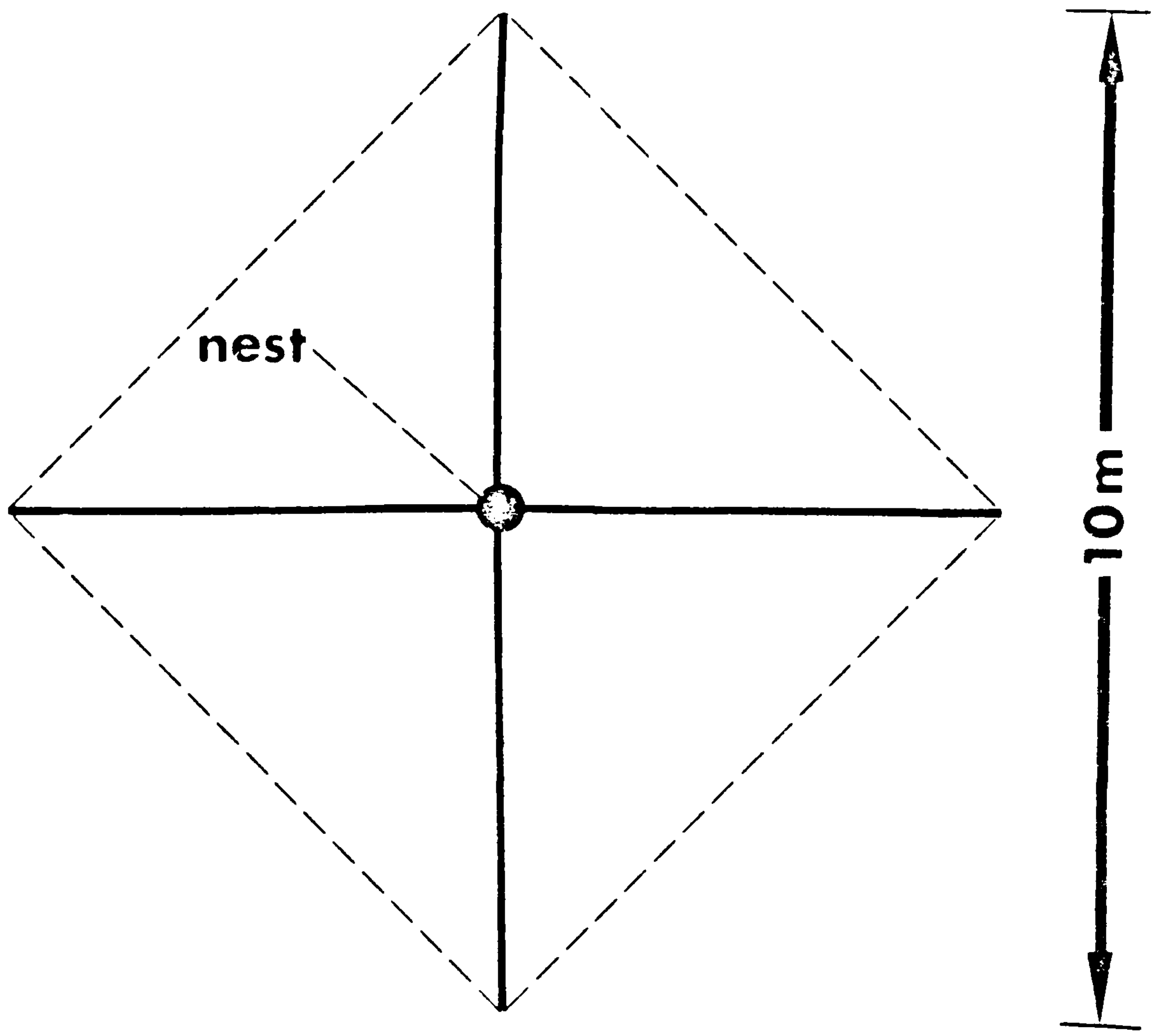

FIGURE 1. Design for analysis of vegetation around woodrat house or den.

RESULTS

Woodrat Distribution

Neotoma mexicana probably occurs throughout the Guadalupe Mountains at elevations above 1500 meters. Mexican woodrats have been collected at the southeastern base of the mountains in Bell Canyon (Davis and Robertson, 1944), on the walls and around the perimeter of Upper Dog Canyon, and in The Bowl (Fig. 2).

Neotoma albigula occurs around the perimeter of the mountains and on the floors of Upper Dog and West Dog Canyons which penetrate the mountain mass. On the west side of the park the white-throated woodrat is found primarily in or along edges of dry washes extending westward from the mountains.

Neotoma micropus has been found only in the southern portion of the park. Specimens have been collected near Williams Ranch Road entrance on the southeastern boundary of the park, in a large dry wash which skirts the north edge of the central ridge of the Patterson Hills, and near Lewis Well in the extreme western area of the park.

Neotoma mexicana and *N. albigula* are in contact around the perimeter of Upper Dog Canyon. In 1901 Bailey (1905) collected one specimen of *N. albigula* in Upper Dog Canyon at 2073 meters (6800 feet). He also collected four specimens of *N. mexicana*, three at 2134 meters and one at 2377 meters. In 1973 both species were captured in a trap line that extended from the canyon floor up the eastern wall. Specimens of *N. albigula* were captured only on the canyon floor and specimens of *N. mexicana* were found from the base of the canyon wall on up the slope. Neotoma mexicana seemed to be the more abundant species. In 1974 no individuals of N. mexicana were collected below an elevation of 2000 meters, approximately 100 meters above the canyon floor. Several specimens of N. albigula were collected 30 to 40 meters above the canyon floor in 1975, indicating a possible upward shift in the zone of contact between the two species. Gehlbach (personal communication) and Scudday (personal communication) reported both N. mexicana and N. albigula in close proximity near Pratt Lodge in McKittrick Canyon in the late 1950's. No woodrats were found during extensive trapping in McKittrick Canyon in 1973 and 1974.

Neotoma micropus and N. albigula are in contact immediately north of the Patterson Hills. North of this area only N. albigula has been captured and south of the area only N. micropus has been collected (Fig. 2). In a wash north of the road which extends due west of Williams Ranch House several N. albigula were collected, but no N. micropus were found. In another wash 400 meters to the south one N. albigula was collected from a house that was central to several houses from which specimens of N. micropus were taken.

House Sites

Houses inhabited by Neotoma albigula were found in a wide variety of sites. In Upper Dog Canyon a large number of houses had been constructed in association with fallen juniper trees or under living junipers. Houses were observed under red barberry (Berberis haematocarpa) and clumps of prickly pear (Opuntia lindheimeri) and cholla (Opuntia imbricata). Around the perimeter of Upper Dog Canyon and for a short

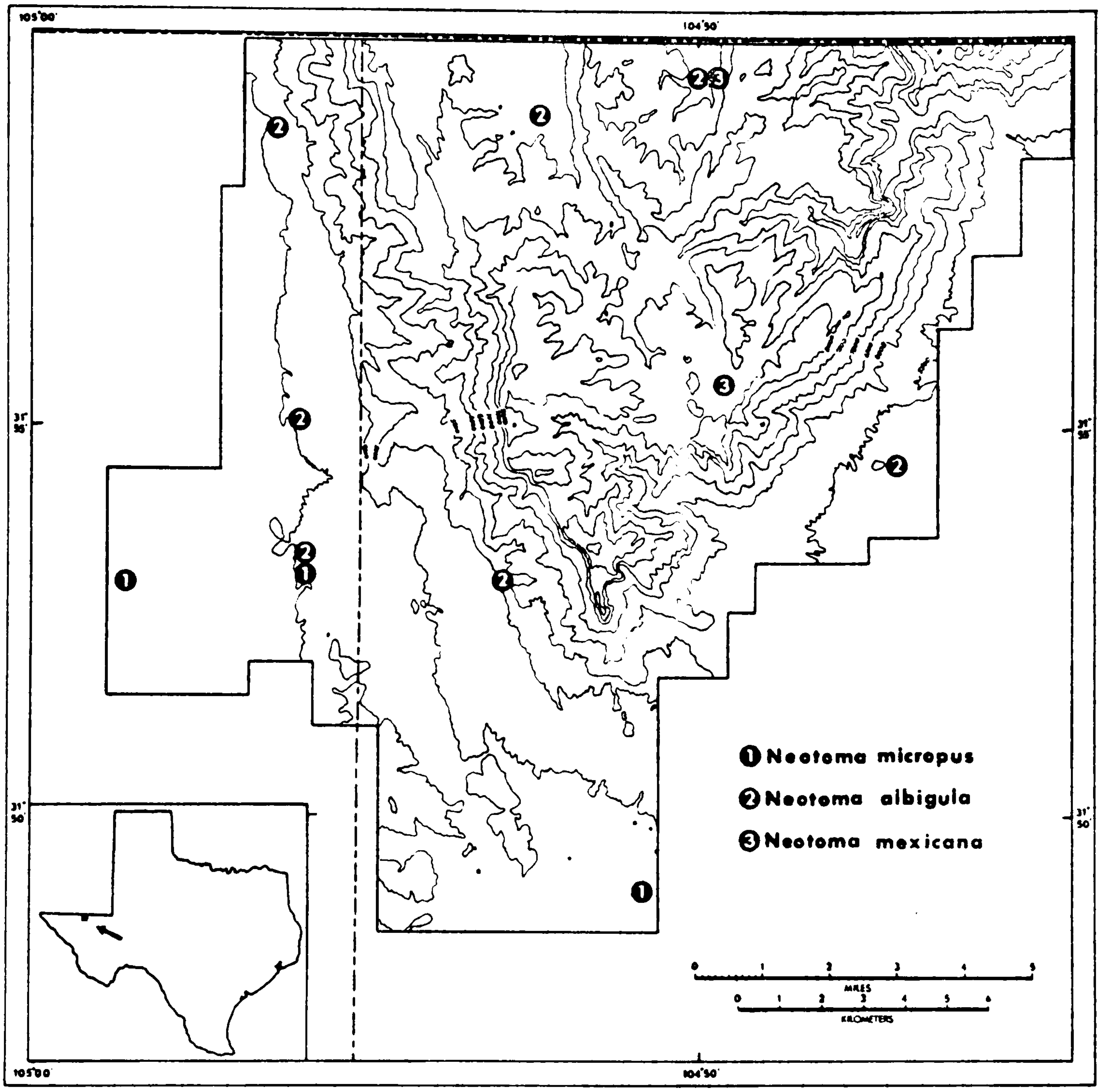

FIGURE 2. Map of woodrat distribution in Guadalupe Mountains National Park.

distance up the slope, _N. albigula_ occurs in rocks utilizing rock crevices for shelter and filling the crevices with sticks, cactus, and debris rather than constructing a house. These rock dens resemble den sites of _Neotoma mexicana_, but appear to have much more material, especially cactus, stuffed into the crevices. In general, houses inhabited by _N. albigula_ in Upper Dog occurred throughout the floor of the canyon wherever suitable shelter was available.

In West Dog Canyon _N. albigula_ houses appeared to be concentrated in or near the dry wash on the canyon floor. Houses were observed under large shrubs, such as red barberry, along the wash. One house was on the edge of the east bank of the wash with a subterranean entrance in the side of the bank about ½ meter below the main house. All houses observed in West Dog Canyon were in very dense shrubby vegetation.

In the Northwest corner of the park all _N. albigula_ houses investigated were situated in large clumps of prickly pear. The cactus clumps were very dense and woodrats had piled cactus joints around the base of the clumps to form houses. This general form of house seems typical for _Neotoma albigula_ on the west side of the park. Large clumps of cactus most often occur in or along edges of dry washes on the west side, on slopes of the Patterson Hills and isolated hills such as the Stage Coach Hills. Large clumps of _Opuntia_ are not common on the creosote bush bajada which dominates the west side of the park. _Neotoma albigula_ houses in large clumps of prickly pear were observed around the Williams Ranch House at the west base of the

Guadalupe escarpment, at a locality northwest of the Ranch House and in the Northwest corner of the park.

Although *Neotoma albigula* houses are predominantly found under large growths of *Opuntia* on the west side of the park, where *N. albigula* was found in close proximity to *N. micropus*, the *N. albigula* house sites were quite different. In this area only one *N. albigula* was collected from a house constructed under a large prickly pear. This house was central to several houses from which specimens of *Neotoma micropus* had been collected. All of these houses were located in the large wash which skirts the north end of the central ridge of the Patterson Hills. In another wash approximately 400 meters to the north several *N. albigula* houses were investigated. Very few cacti are found in this wash and those that do occur are small and scattered. Every active house investigated in this wash was inhabited by an individual of *Neotoma albigula* and all but one were situated under clumps of mesquite (*Prosopis glandulosa*). The remaining house was in a dense growth of *Brickellia laciniata*, a shrubby composite.

On the east side of the park near Nipple Hill, *N. albigula* houses are predominantly under prickly pear or cholla.

A majority of the houses investigated that were inhabited by *Neotoma micropus* had been constructed under large clumps of prickly pear or cholla. Most sites were on the floor or along edges of dry washes. One *N. micropus* was collected from a house on a mesquite hummock near Lewis Well, and several apparently inactive houses were observed on other mesquite hummocks in the vicinity of Lewis Well.

Neotoma mexicana inhabits cliffs and rocks and does not construct a house. These woodrats construct nests in rock crevices and may deposit some plant debris and other materials in crevices, but not to the extent that is characteristic of individuals of N. albigula. In Upper Dog Canyon N. mexicana are found on rocky canyon walls. These woodrats seem to prefer vertical crevices for nest sites, but will utilize deep horizontal crevices with narrow openings.

In The Bowl several Mexican woodrats have been collected in an old log cabin where a nest of shredded paper had been constructed in the far corner of an old bunk. A large number of acorns had been deposited around the nest and an old section of eaves spout was approximately one-third full of acorns. Specimens of N. mexicana were collected on a rock outcrop on a slope above an earthen dam in The Bowl. Woodrat signs were observed along rock outcrops near Bush Mountain and above the Blue Ridge campsite. Although no specimens were taken, these areas are probably inhabited by N. mexicana.

House Analyses

Because Neotoma albigula occurs in a variety of habitats within the park, houses from two distinctly different areas were selected for investigation. Five houses of N. albigula were examined in Upper Dog Canyon and five were examined near the Crossroads immediately north of the Patterson Hills. Four of the houses examined in Upper Dog Canyon had been constructed in association with large fallen juniper trees in an open juniper woodland, whereas the fifth house was located under a large living alligator juniper (Juniperus deppeana) and protected by large red barberry.

Of the *N. albigula* houses investigated near the Crossroads, four were located in a dry wash immediately north of the Crossroads and a fifth was in the large wash which skirts the north edge of the central ridge of the Patterson Hills. Three of these houses had been constructed under spreading many-stemmed mesquite bushes, one was in a dense growth of *Brickellia laciniata*, and one was under a large prickly pear.

Ten houses of *Neotoma micropus* were investigated in the large wash which skirts the north edge of the central ridge of the Patterson Hills. Seven of these houses had been constructed under large prickly pears (*Opuntia lindheimeri* and *Opuntia phaecantha*), one was under a cholla, and one was under a creosote bush (*Larrea tridentata*).

The results of the quantification of house size and weights of materials used in constructing the house are summarized in Table 1. The means are relatively similar except for the mean weights of sticks used in den construction. Analyses of variance (ANOVA) of house lengths, widths, heights, and weights of cholla revealed no significant differences between or among species or localities. Results of ANOVA of weights of sticks in houses are summarized in Table 2. The ANOVA yielded a highly significant F value of 7.1239**. A Student-Newman-Keuls procedure (Table 2) revealed that significantly greater weights of sticks were found in *Neotoma albigula* houses in Upper Dog Canyon than in either *N. albigula* or *N. micropus* houses near the Crossroads. As shown in Table 2, the homogeneous subsets seem to be correlated with locality rather than species.

TABLE 1. Mean house measurements and mean weights of construction components of woodrat houses in Guadalupe Mountains National Park.

Species: Locality:	*N. albigula* (n=5) Upper Dog Canyon		*N. albigula* (n=5) Crossroads		*N. micropus* (n=10) Crossroads	
	Mean	SE	Mean	SE	Mean	SE
House Length	158.4 cm	(19.8115)	106.8 cm	(12.1507)	133.5 cm	(13.6943)
House Width	75.2 cm	(12.9711)	82.2 cm	(8.1704)	84.2 cm	(6.4735)
House Height	37.7 cm	(6.5019)	25.9 cm	(1.7493)	29.15 cm	(3.1056)
Sticks	9.66 kg	(3.1103)	3.45 kg	(0.5508)	2.1 kg	(0.5888)
Cholla	0.99 kg	(0.3509)	0.26 kg	(0.2358)	1.96 kg	(0.6704)
Prickly Pear	0.00 kg	(0.00)	0.02 kg	(0.0120)	0.05 kg	(0.0354)
Manure	0.45 kg	(0.1175)	0.05 kg	(0.0316)	0.21 kg	(0.1234)

TABLE 2. Results of analysis of variance (ANOVA) and Student-Newman-Keuls test (SNK) on weights of sticks in houses of *Neotoma micropus* and *Neotoma albigula*. Means ($\bar{Y}$) are in kilograms.

ANOVA Table

Source	d.f.	MS	F
Among	2	97.7790	7.1239**
Within	17	13.7255	

SNK Test

				Rank 1	Rank 2	Rank 3
			$\bar{Y}$	2.10	3.46	9.66
			n	10	5	5
Rank		$\bar{Y}$	n			
1	*N. micropus*	2.10	10	----		
2	*N. albigula*-Crossroads	3.46	5	1.36ns	----	
3	*N. albigula*-Upper Dog	9.66	5	7.56**	6.20**	----

ns - nonsignificant; ** - $P < 0.01$

The frequency of occurrence of materials accumulated in 20 dismantled houses are presented in Table 3. Note that sticks were found in every house and manure and cactus parts were quite common. Mesquite leaves and pods and tasajillo joints (*Opuntia leptocaulis*) were common in houses near the Crossroads, but absent from houses in Upper Dog Canyon. Juniper parts and acorns were commonly found in houses in Upper Dog Canyon, but were absent in houses from near the Crossroads.

Vegetation Analyses

Floral similarity indices were calculated for the paired comparison of vegetation in the immediate vicinity of each house or den to that of each other house or den. Mean indices between and among species are summarized in Table 4. Note the very low similarity between *Neotoma albigula* plots in Upper Dog and *N. albigula* plots near the Crossroads. This resulted in a mean index among all *N. albigula* plots that was much lower than mean indices among all *N. mexicana* plots and among all *N. micropus* plots. Because of low similarity between *N. albigula* plots in Upper Dog Canyon and *N. albigula* plots near the Crossroads, plots from these two localities were considered separately. The mean similarity index between *N. micropus* plots and *N. albigula* plots near the Crossroads is much higher than the mean index between *N. albigula* plots in Upper Dog Canyon and near the Crossroads.

A modified line-intercept technique was developed to estimate coverages of plant species in the vicinity of a woodrat house, because

TABLE 3. Materials found in woodrat houses and number of houses in which they were found.

	Number of houses		
Species: Locality:	*N. albigula* Upper Dog (n=5)	*N. albigula* Crossroads (n=5)	*N. micropus* Crossroads (n-10)
Sticks	5	5	10
Cholla	5	2	9
Tasajillo	0	1	9
Prickly Pear Pad	2	2	6
Prickly Pear Fruit	0	0	1
Manure	5	4	8
Juniper Leaves	3	0	0
Juniper Berries	2	0	0
Acorns	4	0	0
Barberry Leaves	2	0	0
Pine Needles	1	0	0
Pine Cones	1	0	0
Century Plant Leaves	2	1	0
Mesquite Leaves	0	1	0
Mesquite Pods	2	4	6
Bones	2	0	0
Ocotillo	0	0	2
Yucca Pod	0	1	1
Feathers	0	1	0
Old Under Shorts	0	1	0
Rabbit's Foot	0	1	0

TABLE 4. Mean floral resemblance indices between and among species and localities.

Species Compared	Mean Index	SE
N. albigula / N. albigula	19.9244	3.0848
N. albigula - Upper Dog Canyon / N. albigula - Crossroads	2.7760	0.7900
N. albigula - Upper Dog Canyon / N. albigula - Upper Dog Canyon	40.7840	3.3505
N. albigula - Crossroads / N. albigula - Crossroads	41.9360	3.1781
N. mexicana / N. mexicana	59.8078	1.1697
N. micropus / N. micropus	45.9142	1.9564
N. albigula - Upper Dog Canyon / N. mexicana	12.6594	1.4474
N. albigula - Upper Dog Canyon / N. micropus	4.0648	0.6239
N. albigula - Crossroads / N. mexicana	0.7670	0.2856
N. albigula - Crossroads / N. micropus	38.4232	1.5246
N. mexicana / N. micropus	1.2034	0.2415

the floral similarity index does not reflect frequency or coverage of a particular species within a plot, but merely its presence. To standardize the technique, the nest chamber was used as the midpoint of each transect. Traditional vegetation analysis methods are randomized in order to obtain a random sample, however, the method developed for this study was standardized so that each plot would be sampled in the same manner. It should be noted that the house is not necessarily the center of the resident woodrat's home range. Mean per cent coverages of dominant plant species on plots are listed in Table 5. The per cent of plots on which the species were found is also listed in Table 5. A plant was considered to be dominant only if it was present in 50 per cent or more of the plots. Note that plots around *N. micropus* houses and those of *N. albigula* near the Crossroads have similar dominants with somewhat different coverages. The presence of *Opuntia lindheimeri* as a dominant on *N. micropus* plots in contrast with the absence of that plant on *N. albigula* plots is significant.

In addition to ground coverage, understory cover and canopy cover were also measured. It is theoretically possible, therefore, to record coverages greater than 100 per cent. These results must be interpreted as estimates of plant coverages in relationship to house or den sites and not as random samples of the vegetation of the area. Plots around houses of *N. albigula* in Upper Dog Canyon and near the Crossroads were considered separately because of their low floral similarity indices.

TABLE 5. Dominant plants on woodrat house or den plots, estimated per cent coverages of plant species on the plots, and per cent of sampled plots on which the dominants were found.

Neotoma mexicana (n=10)	Per Cent Coverage	Frequency
Nolina micrantha	11.08	80%
Muhlenbergia pauciflora	9.595	100%
Dasylirion leiophyllum	7.985	80%
Cercocarpus montanus	7.19	90%
Quercus undulata	3.575	80%
Neotoma albigula - Upper Dog Canyon (n=5)		
Stipa tennuissima	23.17	80%
Bouteloua gracilis	3.11	80%
Xanthocephalum sarothrae	2.86	100%
Lycurus phleiodes	2.5	80%
Muhlenbergia repens	1.64	60%
Neotoma albigula - Crossroads (n=5)		
Prosopis glandulosa	17.32	60%
Larrea tridentata	8.38	80%
Brickellia laciniata	6.63	60%
Muhlenbergia porteri	6.48	80%
Setaria leucopila	0.79	80%
Neotoma micropus (n=10)		
Larrea tridentata	17.39	100%
Opuntia lindheimeri	9.71	50%
Prosopis glandulosa	9.54	50%
Muhlenbergia porteri	5.94	60%

DISCUSSION

Woodrat Distribution

The ranges of *Neotoma mexicana*, *N. albigula*, and *N. micropus* overlap in Texas from the Guadalupe Mountains and Davis Mountains westward (Hall and Kelson, 1959). Geographic range descriptions of *Neotoma* can be misleading, because where two or more species of woodrats occur in the same area they often establish distinct zones of contact with little or no overlap. The distribution of woodrats in Guadalupe Mountains National Park conforms to this pattern (Fig. 2). Throughout the vast majority of the park the woodrat distribution is best described as microallopatry with narrow zones and areas of microsympatry. Similar situations have been described in other areas where ranges of two or more species of woodrats overlap (Bailey, 1905; Bailey, 1931; Finley, 1958; Cameron, 1971; Wright, 1973). Reasons for this habitat partitioning are complex and vary depending on species involved and the nature of the habitat.

Finley (1958) reported that ecological distribution of woodrats is primarily determined by climbing ability, house construction ability, and diet. In addition, water economy probably influences distribution (Lee, 1963; Boice and Boice, 1968; Boice, 1969; Birney and Twomey, 1970).

According to Finley (1958) *Neotoma mexicana* is the most agile climber of the woodrats in Guadalupe Mountains National Park followed in ability by *N. albigula* and *N. micropus*. Distributional patterns observed in the park correlate nicely with these reported differences in climbing ability, with N. mexicana inhabiting steep cliffs and rocky slopes, N. albigula occurring from gentler rocky slopes out onto the flats, and N. micropus found only on the flats.

House building activities are apparently correlated with the collecting instinct of woodrats. Finley (1958) reports that N. albigula and N. micropus exhibit strong collecting instincts and are capable of constructing large houses. The collecting instinct of N. mexicana is much weaker relative to the other two species, and individuals of this species do not build houses. Where individuals of N. albigula live in rock crevices in Upper Dog Canyon a large amount of sticks, cactus joints, and other materials have been carried to the den site and stuffed into crevices. Rock dens of N. mexicana in the same area have very little accumulated material.

Food habits studies (Vorhies and Taylor, 1940; Spencer and Spencer, 1941; Finley, 1958; Wood, 1969) suggest that N. albigula and N. micropus utilize cacti and other succulents to a large extent for food. Finley (1958) reported that N. mexicana apparently dislikes cactus.

Interrelationships between desert dwelling species of woodrats and species of cactus (Opuntia spp.) have been well documented (Vorhies and Taylor, 1940; Spencer and Spencer, 1941; Vorhies, 1945; Finley, 1958; Lee, 1963; Raun, 1966; Brown et al., 1972). Opuntia spp. are utilized for shelter, food, and water. Woodrats must depend on vegetation as a source of water because they cannot subsist on metabolic water (Schmidt-Nielsen et al., 1948; Schmidt-Nielsen and Schmidt-Nielsen, 1952). Opuntia is an excellent water source because it has a high water content throughout the year (Lee, 1963) and its cell sap has a low osmotic pressure (Korstian, 1924).

House Analyses

Analyses of representative houses of N. albigula and N. micropus supports preliminary observations that house size and weights of materials used to construct a house are more dependent on availability of materials than on differences in degree of collecting instinct between the two species. Finley (1958) reported that houses of N. albigula and N. micropus found in similar habitats were indistinguishable. The results of this study substantiate that observation. The significant difference in weights of sticks in N. albigula houses in two diverse habitats reflects the opportunistic nature of this species. Differences can probably be attributed to availability of juniper sticks in Upper Dog Canyon where most houses are located in an open juniper woodland.

Although no significant differences were revealed between houses of Neotoma albigula and N. micropus where the two species are microsympatric, there was a striking difference in house sites. Only one N. albigula house was located under a cactus in the zone of contact, while 80 per cent of the N. micropus houses had been constructed under cactus (Opuntia spp.). Olsen (1973) postulates that shelter site selection is based on the criterion of cover near the ground. He found no significant response to stem types.

It is notable that, although cholla was present on only two of the five *N. albigula* plots in Upper Dog Canyon, all houses contained cholla joints (Table 3). Although woodrats can drag cholla joints without much trouble, they have difficulties in handling large prickly pear pads. Prickly pear pads are found in greatest numbers in houses which have been constructed at the base of a living prickly pear. Pads found in other houses were always small. In areas where tasajillo was present, joints and fruits from this cactus were present in 90 per cent of the houses.

Vegetation Analyses

The floral similarity indices computed for this study proved to be useful for preliminary analyses. A low index may indicate that two areas are so dissimilar that no additional analysis is required, but if the index is high, additional statistical techniques may be employed to further analyze the data. An examination of the similarity indices suggested that it would be best to consider the *N. albigula* plots in two different localities separately (Table 4). Vegetation on house plots of *N. albigula* at the Crossroads closely resembled vegetation on house plots of *N. micropus* in the same area, but exhibited little resemblance to plots of *N. albigula* in Upper Dog Canyon. These results are consistent with results of house analyses. With the exception noted above, all indices between species were much lower than indices among species. Although floral similarity does not reflect the frequency or coverage of plant species, it must be noted that the mere presence or absence of a plant species may be more important than its relative abundance.

The modified line-intercept method designed for this study facilitates the description of vegetation in the immediate vicinity of a woodrat house or den. Standardization of the method allows for comparison of vegetation surrounding different houses. Use of perpendicular line-intercepts tends to emphasize plants in the center of the plot and, therefore, emphasizes the plant selected for a house site. This bias was designed into the method, because the plant chosen for a house site often provides shelter, food, and water and, therefore, may be the most important plant in the life of the resident woodrat.

A quadrat method of vegetation analysis was tested during this study, but was not considered to be nearly as satisfactory as the line-intercept method. A manuscript is in preparation that compares the two methods.

Finley (1958) suggests that Neotoma mexicana and N. albigula are sufficiently ecologically divergent to limit interspecies competition. Vegetation data from this study indicate that these two species are found in quite different habitats in Guadalupe Mountains National Park in spite of the fact that they are in close contact around the perimeter of Upper Dog Canyon. The area of microsympatry generally coincides with an ecotone between the chaparral-like vegetation of the canyon wall and the open canyon woodland of the canyon floor. In the absence of N. mexicana, N. albigula could probably inhabit much of the area now occupied by N. mexicana with the possible exception of vertical cliffs. Neotoma mexicana would not invade the canyon floor to a great extent because of the limited number of rocky den sites. Finley (1958) reported that an individual N. mexicana will occasionally invade an unoccupied N. albigula house near a rocky slope, but there is no evidence that Mexican woodrats ever construct a house.

The partitioning of habitat in Upper Dog Canyon is apparently strongly influenced by differences in climbing ability, house building ability, and vegetation requirements or preferences.

There are contrasting reports on the preferred habitat of Neotoma albigula. Bailey (1905) never found N. albigula away from rocky situations in West Texas and describes the species as a cliff dweller. Vorhies and Taylor (1940) found N. albigula in almost every habitat type in the Lower Sonoran zone in Arizona. They were common in the Upper Sonoran zone and present in the Transition zone up to 7000 feet with one specimen taken at 8200 feet in the Santa Rita Mountains. Bailey reported that N. albigula in West Texas apparently belonged to the Upper Sonoran zone, but extended into the Lower Sonoran along cliffs and rocky gulches. A preliminary view of N. albigula distribution in Guadalupe Mountains National Park would lead to the same conclusion. The key to this paradox is the presence of Neotoma micropus in West Texas whereas the distribution of this species does not extend into Arizona.

Finley (1958) could not distinguish between ecological requirements of N. albigula and N. micropus and concluded that they competed for house sites wherever they came in contact. He thought that the two species could coexist at low population levels with little competition, but that with higher populations, competition could become intense. Wright (1973) concluded that competitive exclusion of N. micropus by N. albigula may be occurring where the two species coexist in the Mesilla Valley of New Mexico.

Neotoma albigula occurs in a variety of habitats in Guadalupe Mountains National Park and appears to have less specific habitat requirements than N. mexicana or N. micropus. Where N. albigula and N. micropus are in contact on the west side of the park, N. albigula has apparently shifted to a secondary habitat and diet. Diet studies (Vorhies and Taylor, 1940; Spencer and Spencer, 1941; Finley, 1958; Wood, 1969) suggest that both N. albigula and N. micropus utilize cacti to a large extent for food. Field observations during this study support those suggestions with one significant exception. Cacti were being used for food at every N. micropus house investigated as evidenced by an abundance of partially eaten cactus joints and fruits. This same statement can be made for every N. albigula house observed except those at the zone of contact with N. micropus. Although the mean floral similarity index is relatively high between house plots of the two species in this area, the relative per cent coverages are different. There is one important difference--Opuntia was present at only one of five N. albigula sites examined at the zone of contact. The one plot with Opuntia present was located in the midst of several N. micropus houses. There was no indication whether the house was constructed by the resident N. albigula or whether it had moved into a vacant N. micropus house. In contrast to this area of microsympatry, all other specimens of N. albigula collected on the west side of the park were captured near houses constructed under growths of Opuntia. Where N. albigula and N. micropus are in close proximity, N. albigula houses were located predominantly under mesquite. This apparent shift in habitat selection must be accompanied by a shift in diet. It appears that N. albigula utilizes cactus for food throughout the park except at the zone of contact with N. micropus where cactus are almost totally absent from N. albigula house sites.

The observations discussed above support the principle of competitive exclusion postulated by Gause (1934). Neotoma albigula may be avoiding direct competition with the larger, and possibly more aggressive N. micropus by shifting to a secondary habitat and diet. A similar situation has been described with Neotoma lepida and N. fuscipes in California (Cameron, 1971). It is quite possible that behavioral differences exist between N. albigula and N. mexicana that may be preventing N. albigula from invading areas where N. mexicana is present.

In summary, the distribution of Neotoma albigula in Guadalupe Mountains National Park may be limited more by the presence of the other two species of woodrats than by habitat limitations. The distribution of N. mexicana is limited by availability of favorable habitat, and the distribution of N. micropus is limited by the presence of N. albigula and availability of favorable habitat.

Ecological observations and data from this study are consistent with current systematic interpretations of these three species. *Neotoma albigula* and *N. micropus* are considered to be closely allied (Anderson, 1969; Finley, 1958; Birney, 1973). *Neotoma mexicana* is placed in the same subgenus (*Neotoma*) as *N. albigula* and *N. micropus* (Goldman, 1910), but is not as closely related to the other two species as they are to each other. *Neotoma micropus* is considered intermediate between *N. floridana* and *N. albigula* (Anderson, 1969; Finley, 1958; Birney, 1973) and hybrids are known between *N. floridana* and *N. micropus* and between *N. micropus* and *N. albigula*. Several woodrats live trapped in zones of contact during this study were karyotyped, but no evidence of hybridization was found. All three species found in Guadalupe Mountains National Park can be distinguished karyotypically (Baker and Mascarello, 1969).

Woodrats comprise an important component of the ecosystem in Guadalupe Mountains National Park. They are among the most abundant mammalian species in the park and their role is complex. The following vertebrates that occur in the park have been reported to prey upon woodrats: snakes, hawks, owls, roadrunner, skunks, badger, gray fox, ringtail, coyote, and bobcat (Bailey, 1931; Vorhies and Taylor, 1940; Linsdale and Tevis, 1951; Raun, 1966). Vorhies and Taylor (1940) and Spencer and Spencer (1941) concluded that woodrats consume only small amounts of grasses. Woodrats have often been blamed for the spread of cactus, but there is no evidence to support this accusation. To the contrary, a cactus plant selected as a site for a woodrat house is apparently harmed by debris collected by the rat (Vorhies and Taylor, 1940). Spencer and Spencer (1941) reported that woodrats tend to restrict the spread of cholla. My field observations do not suggest that cactus populations are being harmed to any great extent by woodrat activity. Woodrats are an important food source for carnivores in Guadalupe Mountains National Park. They apparently have a minimal effect on the flora of the park and do not pose a serious threat to the food resources of other animals.

Woodrats as Biological Indicators

One of the primary objectives of this study was to determine the feasibility of using woodrats as biological indicators. Populations of woodrats reflect changes in the vegetation with which they are associated. Numbers of *Neotoma albigula* tend to increase as the result of overgrazing (Vorhies and Taylor, 1940). Heavy grazing may promote growth of *Opuntia* and mesquite by reducing competition from grasses and by reducing frequency of fires by limiting the amount of fuel. Increases in *Opuntia* and mesquite would provide more woodrat shelter sites. Because *N. micropus* prefers similar shelter sites, a similar response to overgrazing would be expected. The decrease in grazing pressure that accompanied the creation of Guadalupe Mountains National Park should result in a decrease in numbers of *N. albigula* and *N. micropus*.

Raun (1966) reported that a large scale die off of prickly pear was accompanied by disappearance of a *Neotoma micropus* population which used cactus for shelter. Loss of vigor and rotting of cactus was apparently caused by four years of abnormally high rainfall.

Wright (1973) postulates that range extension by N. albigula at the expense of N. micropus in the Mesilla Valley of New Mexico is in response to successional changes in vegetational composition due to human activity. Vorhies and Taylor (1940) refer to N. albigula as an "animal weed."

It would be feasible to utilize woodrats as a biological indicator in Guadalupe Mountains National Park. Shifts in the zones of contact between species could be easily detected and would indicate a change in habitat conditions favoring one species over the other. A continued warming trend over a number of years could result in the reduction of Neotoma mexicana habitat on the walls of Upper Dog Canyon. This would facilitate the invasion of N. albigula. The increase in the quality and quantity of grassland in the park should result in reduced abundance of cacti and, therefore, reduced numbers of N. micropus and N. albigula. The grassy meadows in Upper Dog Canyon are fragile. Increased human use in this area will probably damage the grassland resulting in increased numbers of cacti and, therefore, increased numbers of N. albigula. Range extensions and increased numbers of N. albigula may indicate general habitat degradation in the park. This may be caused by human impact, climatic changes, or may be a result of wildlife activity. Species of cactus are severely harmed by fire (Dwyer and Pieper, 1967; Wright, 1972; Heirman and Wright, 1973), thus an increase in frequency of fire, whether naturally or by prescription burning, would reduce the populations of N. micropus and N. albigula.

Although it is evident that woodrats could be useful biological indicators, a combination of monitoring systems would be desirable to detect habitat changes and assess human impact. The monitoring of changes in the vegetation should be of highest priority. Our knowledge of effects of vegetational changes on mammalian populations is limited and this information is necessary in order to make meaningful resource management decisions. Once we know how changes in vegetation are reflected in mammal populations, the distribution and abundance of mammalian species can be predicted from vegetational analyses. The small mammal populations should be periodically monitored, and vegetational changes should be correlated with changes in small mammal demography. To implement such a program, a system of environmental impact monitoring could be designed to include a series of permanent grids for monitoring small mammal populations combined with a plan for monitoring the vegetation on each grid. Data resulting from periodic utilization of this system would be invaluable in assessing human impact, ramifications of changing climatic conditions, and responses to prescribed burning.

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