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WOODRATS AND CHOLLA: DEPENDENCE OF A SMALL MAMMAL POPULATION ON THE DENSITY OF CACTI¹

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Abstract. In the deserts of Southern California, stands of jumping cholla cactus (*Opuntia bigelovii*) are usually inhabited by desert woodrats (*Neotoma lepida*). The density of woodrats is obviously correlated with the density of cacti. On our study area, an alluvial fan in Joshua Tree National Monument, 80% of the variability in the density of woodrats could be attributed to variation in the density of cacti. The turnover of the woodrat population (mortality and replacement) apparently was greatest in areas of low density of cacti. The dependence of woodrat populations on the density of cholla may be attributed to the fact that the cacti provide most resources required by the woodrats: food, water, materials for den construction, and a means of avoiding predation. Woodrats also are abundant in some habitats where there is little or no cactus of any kind, so that their dependence on cholla is not obligate.

The distribution and abundance of a population of small mammals usually depend upon interactions between a number of environmental variables. This makes it difficult to account for temporal or spatial changes in the abundance of most species. Even the causes of enormous cyclic changes in abundance such as those shown by arctic lemmings and other microtine rodents remain obscure after several decades of fairly intensive research (Krebs 1964, Krebs, Keller, and Tamerin 1969, Batzli and Pitelka 1970, Schultz 1964, Chitty 1964). However, the distributions and abundances of several kinds of desert rodents are well correlated with characteristics of the vegetation or the substrate (Rosenzweig and Winakur 1969). Perhaps the most striking example is the relationship between the abundance of woodrats (genus *Neotoma*) and the density of prickly pear and cholla cacti of the genus *Opuntia* (Raun 1966, Vorhies and Taylor 1940). In order to quantify and account for this relationship we studied a population of *N. lepida* on an alluvial fan in Southern California where there was great variation in the density of *O. bigelovii*.

METHODS

The study was made in the Cholla Garden, a stand of *Opuntia bigelovii* on an alluvial fan at an elevation of approximately 610 m in Joshua Tree National Monument, Riverside County, California. Individual cholla plants and adult woodrats were censused on square plots measuring 50 yards (45.7 m) on a side. All *Opuntia bigelovii* above 0.5 m in height were

counted on each plot. The number of woodrats on each plot was determined by counting the number of dens which showed conspicuous sign of occupation. Except when females have unweaned young, only one woodrat occupies each den (Raun 1966, and authors' observations from trapping and excavating dens) so the number of occupied dens provides an accurate estimate of the adult woodrat population. The dens on the study plots were large mounds of cholla joints and other debris (Fig. 1). Dens were readily found, and it was relatively easy to determine which ones were occupied by noting whether the entrances were in good repair and whether there were fresh feces and food materials on the den.

An initial study was made in 1968; the densities of woodrats and cacti were censused on a number of temporary plots on March 12 and June 27. On February 14, 1970, 10 permanent, contiguous plots were laid out along a gradient of cholla density (Fig. 1). The plots extended from an area of high density near the Cholla Garden Nature Trail, southeast to an area where cholla was almost absent. Woodrat dens on the study area were individually marked so that changes in occupancy and construction of new dens could be detected. The number and state of occupation of the dens on the permanent plots were recorded at monthly intervals for a period of 1 year.

RESULTS AND DISCUSSION

In both 1968 and 1970 there was a direct, linear relationship between woodrat density and cholla density (Fig. 2). On the permanent plots (1970) the correlation between woodrat density and cholla density was high ($r = 0.89$ to 0.92 ; $P < 0.001$); thus approximately 80% of the variability (coefficient of determination, $r^2 \cong 0.79$) in the abundance of woodrats is accounted for by the density of cacti. Raun

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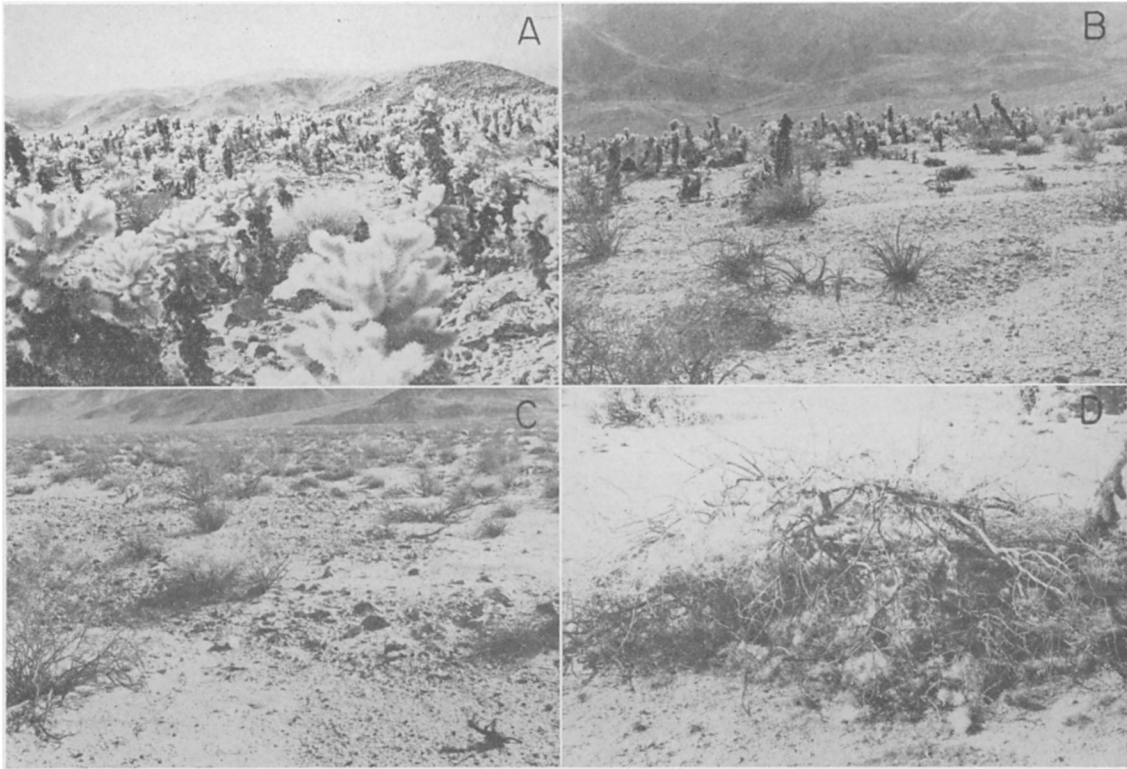


FIG. 1. The study area in the Cholla Garden, Joshua Tree National Monument, showing the variation in the density of cacti (A, B, C) and an occupied woodrat den (D). Note the joints of cholla and piles of spines on the den.

TABLE 1. Changes in occupancy of woodrat dens on the permanent study plots during 1970-71

	Month											
	F	M	A	M	J	J	A	S	O	N	D	J
Occupied dens	20	19	18	19	19	21	24	25	23	23	20	18
Unoccupied dens	30	31	32	31	31	31	29	28	30	30	33	35
Occupied dens abandoned	—	1	2	0	0	0	0	0	1	0	2	2
Unoccupied dens inhabited	—	0	1	1	0	0	0	1	0	0	0	0
New dens constructed	—	0	0	0	0	2	1	0	0	0	0	0

(1966) obtained a similarly high correlation between the density of *N. micropus* and the cover provided by a prickly pear cactus (*O. lindheimeri*). On his study area in southern Texas he also observed an abrupt decline in the woodrat population when most of the cacti were killed during an unusually wet year. In our study area densities of *N. lepida* ranged from 8 per plot (38.3/ha) in the most dense stands of cholla to nearly 0 where cholla was almost absent. These figures compare favorably with maximum densities of 31.1/ha for *N. micropus* in dense prickly pear in southern Texas (Raun 1966) and 49.4/ha for *N. albigula* in cholla in southern Arizona (Spencer and Spencer 1941, Vorhies and Taylor 1940). If we assume a density of 30 woodrats per hectare and an average weight of 100 g for an adult rat, then dense stands of *Opuntia* throughout the southwest support

a biomass of 3 kg/ha of woodrats alone. This figure is three times the value (1.1 kg/ha) obtained by Chew and Chew (1970) for all of the small mammals in a different (creosote shrub) desert community.

During 1970-71 when the plots were visited at monthly intervals, significant changes in the occupancy of dens were noted (Table 1). There were more occupied dens during summer and early fall than there were during winter and spring. During the year eight dens were abandoned, three abandoned dens were refurbished and reoccupied, and three new dens were constructed. The total population of woodrats on the plots declined by two individuals (10%) between February 1970 and January 1971. Abandonment of dens almost certainly represents the deaths of their occupants. Reoccupation of abandoned dens



FIG. 2. Relation between numbers of occupied woodrat dens and numbers of cholla cacti on square plots measuring 50 yards (45 m) on a side.

and construction of new ones presumably represents the establishment of dispersing juveniles, since mature established woodrats are unlikely to move to other dens (Raun 1966). Increases in the population in late summer apparently reflect reproductive recruitment. Young are born in spring and early summer, and they have dispersed and established their own dens by August and September when the number of occupied dens is greatest. Population size declines during late fall, winter, and early spring as a result of mortality in the nonreproductive population.

As shown in Fig. 3, there is an inverse relationship between the proportion of dens which are unoccupied and the density of cacti ($r = .70$, $P < 0.05$ for both 1968 and 1970). This suggests that there is a greater turnover of the population (higher rates of mortality and replacement by dispersing juveniles) where there are fewer cholla. This in turn probably reflects an increased rate of predation where there are fewer cacti to provide cover for the woodrats and to deter predators with their spines. It may also be due in part to a decreased supply of food and water where the cacti are sparsely distributed.

DISCUSSION

The great dependence of local woodrat populations on the density of jumping cholla in our study area and elsewhere in the deserts of Southern Cal-

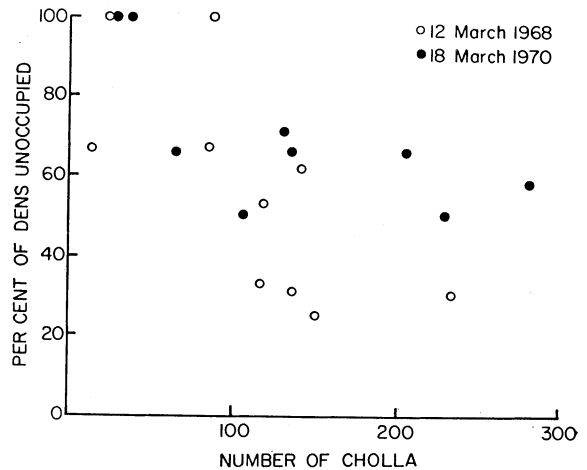


FIG. 3. Relation between the percentage of woodrat dens which were not inhabited and the number of cholla cacti on square plots measuring 50 yards (45 m) on a side.

ifornia can be explained by noting that *Opuntia bigelovii* provides *Neotoma lepida* with four important kinds of resources: food, water, materials for den construction, and protection from predators. When it is abundant, cholla is an important source of food and water for woodrats. They feed on the succulent flesh and discard the spines, which accumulate in huge piles at occupied dens. In addition to cholla, creosotebush (*Larrea divaricata*) is the only important source of food for woodrats in the Cholla Garden area. Joints of cholla are a preferred material for the construction of dens (Fig. 1). Even when the density of cacti is low and the woodrats must travel many meters to obtain joints, cholla is still the most commonly used building material. The cactus-covered dens are armed fortresses which protect inactive woodrats and their dependent young from predators. In addition the dens provide microclimatic temperatures and humidities which permit their occupants to survive the climatic extremes of the desert (Lee 1963, Brown 1968). Finally, in the most dense stands of cholla the woodrats must be largely immune to predation even when they are active outside their dens. In these areas it is virtually impossible to take a step without brushing against a cactus plant or a detached cholla joint lying on the ground. Only the slightest contact with a joint is necessary for its spines to become embedded deeply in flesh (hence the name jumping cholla). In these dense stands of cholla, woodrats have well-developed, cleared trails radiating out from their dens and running under the bases of nearby cactus plants. These trails are lined for much of their length with joints and spines of cholla. It is difficult to imagine how predators could successfully pursue and capture woodrats in areas where the cacti are dense.

Woodrats which live where cholla is abundant have a remarkable set of behavioral and morphological adaptations which permit them to live among and utilize cholla as described above and yet avoid injury by the spines. Bonaccorso and Brown (1972) have shown that cholla joints are a preferred item for den construction, and that they are handled and transported with ease. In addition, the pelage and soles of the feet are highly resistant to penetration by cactus spines and the woodrats have specific, highly specialized behavior patterns which enable them to feed on and move over and around cholla with impunity (Brown, unpublished information).

It is important to emphasize that *Neotoma lepida* is not always dependent on dense stands of *Opuntia bigelovii*. In the more coastal regions of Southern California woodrats attain high densities in dense stands of prickly pear cactus (*Opuntia occidentalis*) (Lee 1963). At many localities in the deserts of Southern California where *N. lepida* is abundant, cacti of all kinds are scarce or absent. When cacti are absent, woodrats are usually most numerous in rocky habitats where large boulders, talus, or numerous cracks provide a great deal of cover (Ryan 1968, Brown, unpublished observations). Again, this suggests that the capacity of a habitat to support woodrats depends upon the extent to which it can afford them protection from predators.

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