Mound Structure in Three Taxa of Mexican Kangaroo Rats (Dipodomys spectabilis cratodon, D. s. zygomaticus and D. nelsoni)

ABSTRACT: Intertaxon variation in eight characters of 83 active burrows of kangaroo rats (*Dipodomys spectabilis cratodon*, *D. s. zygomaticus* and *D. nelsoni*) was studied in the Mexican states of Chihuahua, Zacatecas and Coahuila. Six characters exhibited significant intertaxon heterogeneity. Mounds constructed by *D. s. cratodon* were significantly smaller in diameter and height, those of *D. s. zygomaticus* were significantly closer together, and those of *D. nelsoni* had significantly more total openings and active openings and significantly smaller average diameter of inactive openings, than those of the other taxa. The two subspecies of *D. spectabilis* construct mounds that are more similar to each other than either is to *D. nelsoni*. Burrow structure may be a useful taxonomic character.

INTRODUCTION

Taxonomic relationships between *Dipodomys nelsoni* and *D. spectabilis* have been examined (*see* Best, in press). Baker (1956), Anderson (1972), and Matson (1980) separated these taxa into distinct species, though Nader (1978) considered them conspecific because of morphologic similarities. While a great deal is known about the ecology of *D. spectabilis* (Vorhies and Taylor, 1922), little ecologic information is available for *D. nelsoni* (*e.g.*, Baker, 1956; Anderson, 1972). Though they are morphologically similar, it would be useful to evaluate ecologic parameters, such as the structure of their burrows, which is closely related to functional morphology and behavior.

Intraspecific comparisons of burrows have been made among populations of *Dipodomys agilis* in Baja California (Best, 1982); however, no studies have compared burrow structure between species of *Dipodomys*. Previous accounts have described characteristics of the large earthen mounds constructed by *D. spectabilis* (*e.g.*, Vorhies and Taylor, 1922; Taylor, 1930; Best, 1972; Schroder and Geluso, 1975; Moroka *et al.*, 1982), but only Baker (1956) has described mounds built by *D. nelsoni*. The purposes of this study were to determine the density and surface attributes of mounds for two subspecies of *D. spectabilis* (*cratodon* and *zygomaticus*) and for *D. nelsoni* and to determine differences and similarities among these taxa.

METHODS AND MATERIALS

We analyzed eight mound characters of kangaroo rats at three localities in N-central Mexico. Maximum diameter (greatest distance across the area elevated to form the mound) and height (distance the mound projected above the unexcavated surface near the mound) were recorded to the nearest cm, number of active openings was determined by examination of tracks or tail prints at burrow openings, diameter of active and inactive burrows was measured to the nearest millimeter, and distance to the nearest mound was determined to the nearest meter. Fifteen active burrows systems of *Dipodomys spectabilis cratodon* were examined 10 km NE Villa de Cos, Zacatecas, 46 burrows of *D. spectabilis zygomaticus* were examined 18.4 km ENE Hidalgo del Parral, Chihuahua, and 22 burrows of *D. nelsoni* were examined 7.2 km W General Cepeda, Coahuila. While no attempt was made to quantify characteristics of soil and vegetation, both features were assessed qualitatively. Soils were hard-packed sandy loam and appeared equally friable at all sites. We studied burrows of *D. s. cratodon* in a dense cactus (*Opuntia*) and shrub forest (*Acacia*, *Larrea*, etc.), *D. s. zygomaticus* in an open grassland (*Bouteloua*) with scattered catclaw (*Acacia*), and *D. nelsoni* in an area dominated by scattered creosote bush (*Larrea*), catclaw and cactus.

Character heterogeneity among taxa was tested using a one-way analysis of variance, and a sums of squares simultaneous test procedure to determine maximally nonsignificant subsets (SS-STP; Gabriel and Sokal, 1969). Mean measurements of each character for each taxon were used in multivariate procedures. Characters were standardized (so that each had a mean of 0 and a standard deviation of 1 across taxa), and correlation and distance matrices were calculated (Sneath and Sokal, 1973). Clusters of taxa and characters were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a correlation matrix among characters, and projections of the taxa were plotted on the first three components. To elucidate correlations among characters, dendrograms were constructed from correlation matrices of the eight standardized characters. Statistical analyses were performed at The University of New Mexico Computer Center using the programs UNIVAR (D. M. Power, unpublished) and NT-SYS (Rohlf *et al.*, 1974).

RESULTS

Character correlations.—Diameter and height of all mounds were highly correlated with each other ($r=0.95$), as were total number of openings, number of active openings and number of inactive openings ($r>0.96$). The least correlated characters were the distance to the nearest mound, average diameter of active openings and average diameter of inactive openings ($r<0.51$). Thus, our character set represented traits that were relatively heterogeneous.

Intertaxon variation.—Density of mounds was 5.6 per ha for *Dipodomys spectabilis cratodon*, 13.5 per ha for *Dipodomys s. zygomaticus* and 12.9 per ha for *D. nelsoni*. The smaller number of burrows examined for *D. s. cratodon* may be related to the difficulty in locating burrows in the dense cactus forest of southern Zacatecas.

Significant intertaxon heterogeneity was shown by six of eight characters (Table 1). Only diameter of active openings and number of inactive openings were not significantly different among taxa. As evidenced by the *F*-ratios, total number of openings and number of active openings exhibited the most intertaxon variation, whereas diameter of mound and average diameter of inactive openings exhibited the least, *i.e.*, of those showing significant intertaxon variation.

Dipodomys spectabilis cratodon had larger average diameter of inactive openings and distance to nearest mound (Table 2). Mounds constructed by this taxon were significantly smaller than the other taxa in diameter and height (Table 1).

Mounds constructed by *Dipodomys spectabilis zygomaticus* had greatest diameters and greatest average diameters of active openings (Table 2). This taxon had the smallest means for total number of openings, numbers of active and inactive openings, and distance to the nearest mound. *Dipodomys s. zygomaticus* was significantly different from the other two taxa in having the shortest distance between mounds (Table 1).

Dipodomys nelsoni had largest means for height of mound, total number of openings, and numbers of active and inactive openings, and the smallest means for average diameter of active and inactive openings (Table 2). Statistically significant differences were shown by its largest means for total number of openings and number of active openings, and its smallest mean for average diameter of inactive openings (Table 1).

Multivariate analyses.—Phenograms were constructed from correlation and distance matrices derived from means of the eight characters. The correlation phenogram was divided into two clusters at a correlation of -0.55. One cluster contained the two subspecies of *Dipodomys spectabilis* and the other contained *D. nelsoni*; the cophenetic correlation coefficient was 0.78. For the distance phenogram, the same clusters were present. The subspecies of *D. spectabilis* were sepa-

TABLE 1.—Variation in mounds constructed by kangaroo rats in Mexico. Statistically homogeneous subsets derived from SS-STP analysis are shown by lines below the taxa which are ranked by mean. One asterisk (*) indicates P≤0.05 and two asterisks (**) indicate P≤0.01

Character	*F*-ratio	Taxa		
Diameter of mound	6.586*	*D. s. zygomaticus*	*D. nelsoni*	*D. s. cratodon*
Height of mound	25.960**	*D. nelsoni*	*D. s. zygomaticus*	*D. s. cratodon*
Total no. of openings	120.562**	*D. nelsoni*	*D. s. cratodon*	*D. s. zygomaticus*
No. active openings	100.649**	*D. nelsoni*	*D. s. cratodon*	*D. s. zygomaticus*
No. inactive openings	1.998	*D. nelsoni*	*D. s. cratodon*	*D. s. zygomaticus*
Ave. diameter of active openings	1.352	*D. s. zygomaticus*	*D. s. cratodon*	*D. nelsoni*
Ave. diameter of inactive openings	8.074**	*D. s. cratodon*	*D. s. zygomaticus*	*D. nelsoni*
Distance to nearest mound	10.258**	*D. s. cratodon*	*D. nelsoni*	*D. s. zygomaticus*

rated from *D. nelsoni* at a phenetic distance of 1.49, and the cophenetic correlation coefficient was 0.98.

Loadings of characters on the first three component axes showed total number of openings, number of active openings, and number of inactive openings to have correlations greater than 0.95 on the first component axis, and average diameter of inactive openings had a correlation of -0.99 on this axis. The highest positive loading on the second component was for distance to nearest mound ($r = 0.99$), and highest negative loadings were for diameter of mound, height of mound, and average diameter of active openings ($r > -0.76$). No characters showed loadings on the third principal component. The phenetic variance represented on component one was 60.7% and 39.3% was represented on component two.

Loadings of taxa on the first two axes placed *Dipodomys nelsoni* well away from the two subspecies of *D. spectabilis*. On component one, *D. nelsoni* had a loading of 0.89, *D. s. zygomaticus* −0.53 and *D. s. cratodon* −0.36. The second component had loadings of −0.08 for *D. nelsoni*, −0.59 for *D. s. zygomaticus*, and 0.66 for *D. s. cratodon*. The closest taxa were *D. s. zygomaticus* and *D. s. cratodon* (1.26), and *D. nelsoni* was closest to *D. s. cratodon* (1.46).

DISCUSSION

Our reports of exterior dimensions, burrow characteristics and spacing of the mounds constructed by *Dipodomys spectabilis* agree with previous observations (*e.g.*, Vorhies and Taylor, 1922; Taylor, 1930; Schroder and Geluso, 1975; Moroka *et al.*, 1982). However, we found mounds constructed by *D. s. cratodon* were not as tall, as wide, or as close together as those of *D. s. zygomaticus*. This indicates geographic variation in mound characteristics of *D. spectabilis*. Best (1982) described geographic variation in burrow characteristics of *D. agilis* in Baja California and related the variation to environmental and morphologic attributes. Mean body measurements (in mm) of *D. nelsoni* and *D. s. zygomaticus* from Chihuahua, respectively, are: total length, 308.1, 335.6; length of tail, 180.1, 193.7; length of hind foot, 46.8, 51.4; length of ear, 14.9, 16.4; and body weight (in g), 84.7, 116.5 (Anderson, 1972). Perhaps body size is related to differences in burrow characteristics, because there is geographic variation in morphology within *D. spectabilis* (Nader, 1978). However, we do not have data that would allow comparisons similar to those made by Best (1982).

Though no previous studies have reported dimensions of *Dipodomys nelsoni* mounds, we expected them to be similar to those of *D. spectabilis* because of morphologic similarities, and they were. However, *D. nelsoni* differed significantly from the two subspecies of *D. spectabilis* in total number of exterior openings, number of active openings, and average diameter of inactive

TABLE 2.—Means (standard deviation; range) of eight burrow characteristics of three taxa of kangaroo rats from Mexico

Character	*D. s. cratodon*	*D. s. zygomaticus*	*D. nelsoni*
Diameter of mound (cm)	281.8 (47.7; 190-380)	373.2 (97.5; 192-630)	366.6 (81.4; 220-525)
Height of mound (cm)	18.4 (5.1; 10-25)	41.6 (11.5; 20-66)	50.3 (19.8; 20-84)
Total no. of openings	5.7 (2.4; 2-10)	4.3 (1.9; 1-8)	13.5 (3.1; 8-20)
No. active openings	3.6 (2.2; 1-7)	2.6 (1.2; 1-5)	10.8 (3.7; 4-17)
No. inactive openings	2.1 (1.8; 0-6)	1.7 (1.7; 0-6)	2.7 (2.5; 0-7)
Diameter of active openings (cm)	7.6 (1.5; 5.1-10.0)	8.1 (1.7; 4.8-11.4)	7.6 (1.1; 5.5-9.4)
Diameter of inactive openings (cm)	7.3 (2.1; 3.2-10.5)	7.2 (2.3; 2.5-12.0)	4.8 (0.9; 3.5-7.3)
Distance to nearest mound (m)	19.6 (12.4; 5-41)	10.5 (4.0; 5-19)	15.6 (7.7; 5-33)

openings. These differences were not apparent in the field, but upon examination of photographs of the mounds the differences were conspicuous in most cases. Though there were no statistical differences in spacing of mounds between *D. nelsoni* and *D. s. cratodon*, mounds of *D. nelsoni* appear less abundant. It is likely that mounds of *D. s. cratodon* were more abundant than our data indicate because they were located among dense stands of *Opuntia* and shrubs in Zacatecas. Based upon our qualitative observations, mounds constructed by *D. nelsoni* in dirt piles along Hwy. 137 between General Cepeda and Parras, Coahuila, were much closer together than those in the adjacent creosote bush desert where we studied them. In addition to possibly more favorable soil conditions along the roadway, the larger concentration of mounds there may be related to the distribution of windblown seeds that serve as a source of food.

Multivariate analyses placed the two subspecies of *Dipodomys spectabilis* closer to each other than either was to *D. nelsoni*. If there was clinal geographic variation in burrow characteristics among the three taxa, *D. nelsoni* should have been placed between the subspecies of *D. spectabilis*. Geographically, the sample of *D. nelsoni* is between those of *D. spectabilis*. Our observations indicated the habitats of *D. nelsoni* and *D. s. zygomaticus* were similar, and the habitat of *D. s. cratodon* was very different from both of them. Results of our analyses lend credibility to the taxonomic separation of *D. nelsoni* from *D. spectabilis*.

The taxonomic relationship of *Dipodomys spectabilis* and *D. nelsoni* has been addressed in terms of variation in cranial morphology (see Best, in press), but our study is the first to assess variation in burrow characteristics between these species. The separation of *D. nelsoni* from *D. spectabilis* on the basis of three burrow characters using univariate statistics and the placement of the two subspecies of *D. spectabilis* together and separated from *D. nelsoni* in the multivariate analyses provide additional evidence that these taxa are distinct.

The difference in size of the inactive burrow openings could be because there are different mammals associated with *D. nelsoni* than with *D. spectabilis*; associated species would play a role in modifying or constructing burrows. The greater total number of burrow openings and number of active openings for *D. nelsoni* as compared to *D. spectabilis* may be related to environmental parameters that require more ventilation within the burrow system, or the soil is more friable where *D. nelsoni* occurs. Whatever the causes of the differences between *D. spectabilis* and *D. nelsoni*, they clearly exist. If these differences exist throughout the ranges of these species, they would represent ecologic and behavioral differentiation. Additional study is needed to determine the extent of ecologic variation within and between *D. nelsoni* and *D. spectabilis*; we have shown that differences exist in burrow characteristics of these species in N-central Mexico.

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