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INTRASPECIFIC MORPHOLOGIC VARIATION IN ORD'S KANGAROO RAT, *DIPODOMYS ORDII*, FROM OKLAHOMA

The easternmost portion of the range of Ord's kangaroo rat, *Dipodomys ordii*, extends along the floodplain of the South Canadian River in Oklahoma as far eastward as Pottawatomie County. Distribution is limited to sandy soils along low-lying parts of the floodplain; the species was not encountered on adjacent clay-like soils. These sandy areas are composed of small, partially stabilized dunes that vary in size up to several hectares and are subject to rather constant change by wind and water. In Cleveland and McClain counties, populations of *D. ordii* fluctuate dramatically as the river rearranges suitable habitat or as suitable habitat stabilizes and becomes covered with vegetation. Along the floodplain, only small islands (active sand dunes or blowouts on stabilized dunes) of suitable habitat exist; because these islands may be several kilometers apart, populations inhabiting them appear to be isolated from other populations. Specimens of this species in western Oklahoma (*D. o. richardsoni*) are large and dark colored while those in the extreme easternmost part of the range (*D. o. oklahomae*) are small and pale. Because of the varying degree of isolation and the large amount of morphologic variation in this species in such a limited area, it is an ideal subject for studying the processes that cause intraspecific variation.

Several investigators have noted morphologic variation in *D. ordii* along the South Canadian River. Trowbridge and Whitaker (1940) described *D. oklahomae* and reported that this species was not known to intergrade with any other named kinds. Davis (1942) and Setzer (1949) considered *D. oklahomae* as a differentiated race of *D. ordii*. Best and Schnell (1974) studied age variation in bacula from specimens collected near Norman, Oklahoma, but they made no comparisons with adjacent populations.

We studied intraspecific variation in morphologic characters of *D. ordii* along the South Canadian River in Oklahoma to provide additional insight into the nature of intraspecific variation.

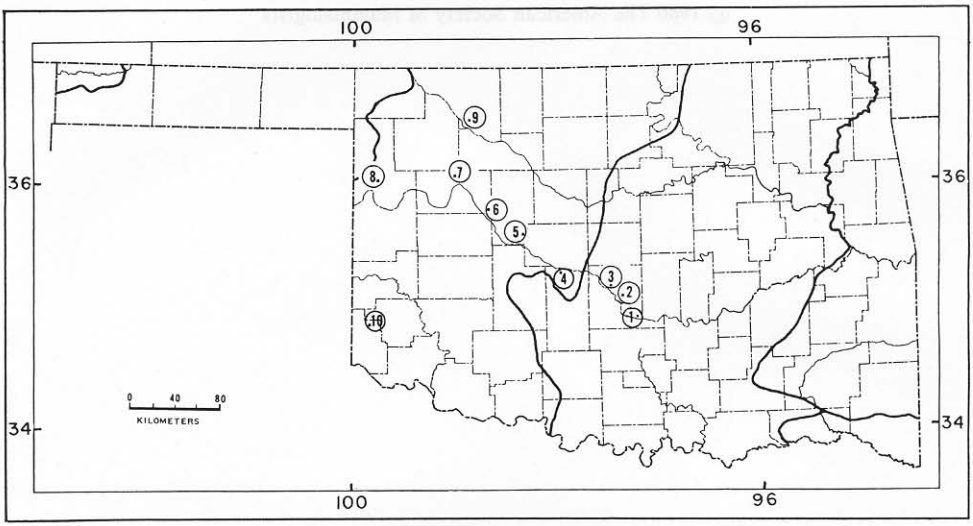

FIG. 1.—Oklahoman localities for the *Dipodomys ordii* used in this study of intraspecific variation. 1) 1.5 mi NW Noble, McClain Co.; 2) west side South Canadian River, across from Norman Dump, McClain Co.; 3) Norman, ¼ mi E Interstate-35 S bridge, McClain Co.; 4) 3 mi N Minco, Canadian Co.; 5) 5 mi N Hinton, Canadian Co.; 6) 5 mi SE Fay, Custer Co.; 7) 1 mi N Taloga, Dewey Co.; 8) 23 mi S Arnette, Ellis Co.; 9) 2 mi W Waynoka, Woods Co.; 10) Harmon Co.

From May 1975 through April 1976, 218 adult *D. ordii* were live-trapped from 10 Oklahoman localities (Fig. 1) and transported to Memphis State University for analysis. All specimens were deposited in the Memphis State University Museum of Zoology.

We recorded 16 linear cranial measurements for each adult specimen. Measurements were taken with dial calipers to the nearest 0.1 mm. Skull measurements and aging criteria were those of Kennedy and Schnell (1978). Because 4 of the 16 measurements we used were statistically invariant (basal length, maxillary width, premolar width, greatest interparietal width), we followed Sneath and Sokal (1973) in removing these measurements from the character set. The final character set contained 12 characters (Table 1). For detailed descriptions of all characters see Kennedy and Schnell (1978).

Because none of the original 16 skull characters examined showed significant sexual dimorphism ($P \leq 0.05$), sexes were combined in the subsequent statistical analyses. Univariate and multivariate biometric routines were employed to analyze the character set. Means of characters are included in Table 2. Standard statistics, single-classification analysis of variance tests, and sum of squares simultaneous test procedures (SS-STP) were carried out with a program (UNIVAR) written by D. M. Power. Some multivariate analyses were performed using NT-SYS (Rohlf et al., 1969). Matrices of Pearson's product-moment correlation coefficients were computed and phenetic distance coefficients were derived from standardized character values. We clustered characters using the unweighted pair-group method using arithmetic averages on the correlation matrix. Also, we extracted the first three principal components; projections of localities were prepared from these data. A shortest minimally connected network was computed in the original character space and was used to connect most-similar localities in the three-dimensional plots. A further explanation of these techniques, plus the rationale for their use, is given in Sneath and Sokal (1973).

Discriminant function analysis was performed using the Statistical Package for the Social Sciences (Nie et al., 1975). To display intraspecific variation graphically, we used the SYMVU program at Memphis State University. All computations were carried out on the Xerox Sigma IX computer at Memphis State University.

TABLE 1.—*Interlocality variation in 12 cranial characters in* Dipodomys ordii *derived from a single-classification analysis of variance.*

Character	d.f.	*F* ratio*
Greatest skull length	9,186	9.536
Bullar-premaxillary length	9,201	4.145
Greatest skull width	9,200	10.531
Greatest skull depth	9,206	17.333
Intermaxillary width	9,194	2.020
Third molar width	9,201	2.882
Toothrow length	9,206	5.940
Upper diastemal length	9,202	4.052
Least interorbital width	9,193	6.701
Nasal length	9,188	4.072
Rostral width	9,189	2.899
Least supraoccipital width	9,206	9.305

* $P \leq 0.05$ for *F* ratios exceeding 1.88.

We found no sexual dimorphism in characters used in this study. Desha (1967), Schmidly (1971), Shaver (1973), and Kennedy and Schnell (1978) reported significant sexual dimorphism in *D. ordii*. Schmidly and Hendricks (1976) found only a limited degree of sexual dimorphism in southern populations of Ord's kangaroo rat. Schmidly (1971) indicated that sexual dimorphism varied geographically, and our results support this conclusion. For a more detailed discussion of sexual dimorphism in this species see Kennedy and Schnell (1978).

A dendrogram computed from the matrix of correlations of skull characters is presented as Fig. 2. Least supraoccipital width, third molar width, nasal length, and intermaxillary width added

TABLE 2.—*Interlocality variation in means of 12 cranial characters for* Dipodomys ordii. *Nonsignificant subsets derived from SS-STP analysis are shown by lines below the locality numbers and ranked means.*

Character	Results of SS-STP analysis									
Greatest skull length	8	9	6	10	5	7	4	3	1	2
	39.48	39.45	39.37	39.24	39.08	39.05	38.50	38.30	38.20	38.02
Bullar-premaxillary length	6	9	10	8	7	5	4	3	2	1
	36.09	35.89	35.86	35.80	35.74	35.57	35.49	35.09	34.94	34.82
Greatest skull width	10	8	6	9	7	5	1	4	3	2
	24.37	24.19	24.10	24.09	23.78	23.48	23.42	23.40	23.25	23.21
Greatest skull depth	6	10	8	9	7	5	1	4	3	2
	12.96	12.95	12.93	12.89	12.88	12.76	12.58	12.52	12.39	12.38
Intermaxillary width	8	10	5	7	9	2	6	3	1	4
	5.46	5.45	5.43	5.41	5.40	5.35	5.32	5.29	5.27	5.21
Third molar width	10	9	7	5	3	8	4	1	6	2
	1.07	0.98	0.97	0.96	0.96	0.96	0.95	0.94	0.94	0.93
Toothrow length	10	6	5	8	7	9	3	1	4	2
	7.87	7.76	7.72	7.69	7.69	7.64	7.56	7.54	7.49	7.46
Upper diastemal length	6	7	8	5	9	3	4	10	2	1
	9.19	8.88	8.87	8.86	8.84	8.73	8.73	8.69	8.69	8.42
Least interorbital width	6	5	8	10	4	7	9	3	2	1
	13.28	13.22	13.12	13.09	13.05	12.96	12.90	12.64	12.55	12.36
Nasal length	8	9	6	7	5	3	1	10	2	4
	14.88	14.70	14.66	14.61	14.45	14.40	14.37	14.36	14.24	14.19
Rostral width	6	5	7	10	8	4	9	2	3	1
	4.09	4.06	4.03	4.00	4.00	3.99	3.90	3.88	3.86	3.38
Least supraoccipital width	1	2	3	5	7	10	9	6	4	8
	3.60	3.34	3.33	3.03	3.01	2.95	2.89	2.84	2.83	2.77

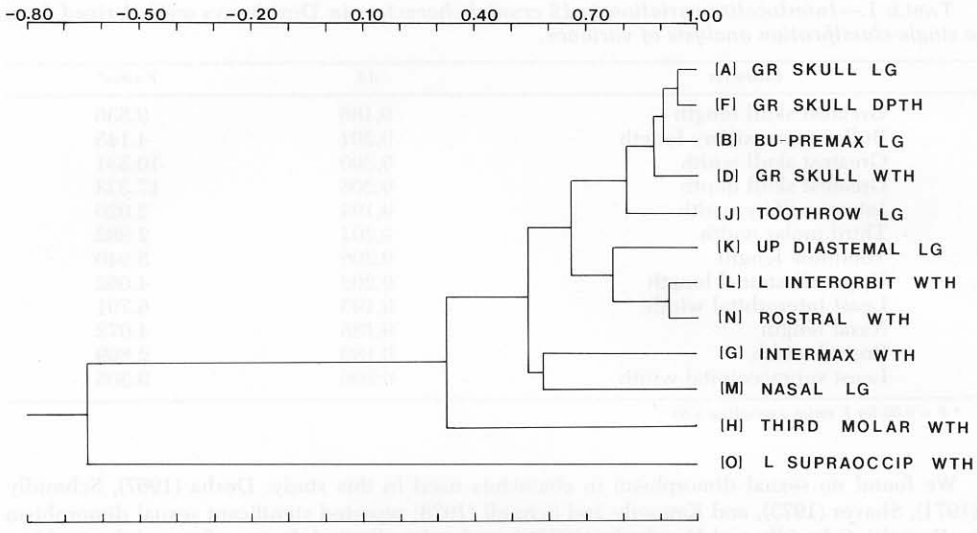

FIG. 2.—Dendrogram that summarizes the variation between characters for *Dipodomys ordii*. Letters enclosed in parentheses correspond to those in Fig. 1 of Kennedy and Schnell (1978).

the most heterogeneity to the character set. The other characters formed a large cluster which can be viewed as two small clusters. Upper diastemal length, least interorbital width, and rostral width group together; greatest skull length, greatest skull depth, bullar-premaxillary length, greatest skull width, and toothrow length formed a second group. The arrangement of the 12-character set used in this study is similar to the 16-character set used by Kennedy and Schnell (1978). However, there is some rearrangement, and the overall correlations of characters in the 12-character set in our study are lower than those reported by Kennedy and Schnell (1978). This indicates that by removing the invariant characters the amount of overlap of information in the character set was reduced.

Kennedy and Schnell (1978) found least supraoccipital width and third molar width to add variation to their character set and have discussed these characters as well as others. However, intermaxillary width and nasal length appear to increase variation in our character set more than in the character set of Kennedy and Schnell (1978). Best (1978) found intermaxillary width to be a useful character in studying the *heermanni* group of *Dipodomys*. Because this dimension reflects breadth between toothrows, it could be a feature (as with third molar width) that reflects an adaptation related to food habits.

Setzer (1949), Nader (1964), Desha (1967), Schmidly (1971), Brownlee (1973), Best (1978), and others have found nasal length to be a useful character when differentiating kangaroo rats. Setzer (1949) indicated a correlation between the decrease in length of the nasals and in width of the rostrum and the mean annual relative humidity of the environment. We were unable to test this correlation because we did not have accurate environmental data.

In general, the skull measurements we used are ones proven useful by other investigators. Although there is some redundancy in the character set as indicated by the high correlations among several characters (Fig. 2), we believe that each character contributed useful information to the study.

Significant interlocality (geographic) variation is shown by each of the 12 characters we used (Table 1). Relative to the degree of intraspecific variation, greatest skull depth, greatest skull width, greatest skull length, and least supraoccipital width exhibited the greatest interlocality variation; intermaxillary width, third molar width, and rostral width had the lowest F-values. Desha (1967) reported greatest skull length and greatest skull depth to have low coefficients of variation, and Schmidly (1971) found greatest skull length and greatest skull depth to be among his least variable cranial measurements. Kennedy and Schnell (1978) reported greatest skull

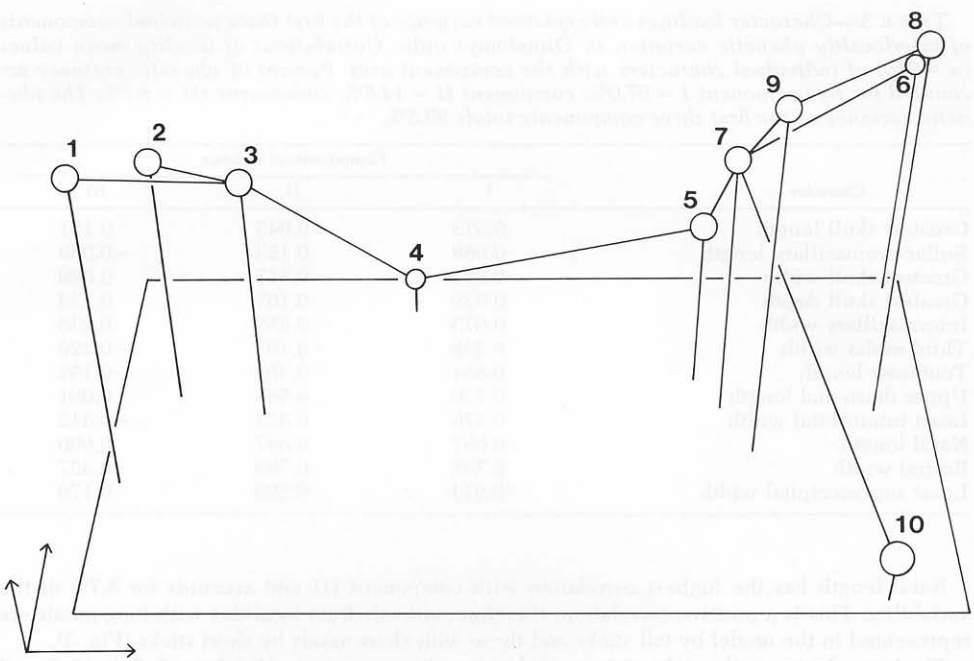

FIG. 3.—Projection of 10 localities onto the first three principal components of variation in the matrix of correlations of 12 skull characters of *Dipodomys ordii*. See Fig. 1 for locality numbers. Shortest minimally connected network values between localities: 1–3 = 0.705; 3–2 = 0.480; 3–4 = 0.947; 4–5 = 1.136; 5–7 = 0.456; 7–9 = 0.564; 9–8 = 0.542; 7–6 = 0.861; 7–10 = 1.047.

length and greatest skull depth to be among the most variable of their character set while the third molar width exhibited the least interlocality variation.

Our results corroborate the finding of Johnston and Selander (1971) that the pattern of size variation extracted from a matrix of size characters depends upon the covariant set selected. Results of SS-STP analyses illustrating these trends for each character are presented in Table 2. The broad pattern of variation over the range for individual characters studied is complicated, but animals from western localities generally are larger while those from more eastern localities are smaller.

Principal components, to summarize character variation among localities, and three-dimensional projections of these for the 10 localities are shown in Fig. 3. Loadings, which indicate the correlations of characters with the first three principal components, are given in Table 3. The first three components explain 90.3% of the total interlocality phenetic variance. Thus, there is little distortion in distances when reducing the 12-dimensional character matrix to three dimensions.

Component I is a size factor with high positive correlations for all but two characters: third molar width and a high negative correlation with least supraoccipital width (values greater than 0.675 were considered high). It separated relatively small *D. ordii* (those to the left in Fig. 3) from larger animals (located to the right). The geographic pattern of projections on component I are summarized in Fig. 4. Largest animals are indicated by high peaks (e.g., 6 and 8), smallest by low peaks (e.g., 1 and 2). This component accounts for 67.0% of the total variation.

Component II has high positive loadings (values above 0.458 were considered high) for upper diastemal length and high negative loadings for third molar width and intermaxillary width—it explains 14.6% of the variation. Animals from localities placed near the front of the model have relatively wide third molars and intermaxillaries and short upper diastemata (Fig. 3). Those with the opposite condition are placed near the back of the figure.

TABLE 3.—*Character loadings and explained variance of the first three principal components of interlocality phenetic variation in* Dipodomys ordii. *Correlations of locality mean values (n = 218) of individual characters with the component axes. Percent of phenetic variance accounted for by component I = 67.0%; component II = 14.6%; component III = 8.7%. The phenetic variance of the first three components totals 90.3%.*

Character	Components of variance		
	I	II	III
Greatest skull length	0.973	−0.045	0.151
Bullar-premaxillary length	0.968	0.123	−0.069
Greatest skull width	0.881	−0.317	0.099
Greatest skull depth	0.939	−0.167	0.139
Intermaxillary width	0.675	−0.458	0.235
Third molar width	0.438	−0.765	−0.426
Toothrow length	0.854	−0.350	−0.152
Upper diastemal length	0.730	0.588	0.081
Least interorbital width	0.876	0.323	−0.312
Nasal length	0.697	0.047	0.696
Rostral width	0.792	0.389	−0.327
Least supraoccipital width	−0.844	−0.299	0.179

Nasal length has the highest correlation with component III and accounts for 8.7% of the variability. This is a positive correlation; therefore, animals from localities with long nasals are represented in the model by tall sticks and those with short nasals by short sticks (Fig. 3).

The large cluster on the right of the model in Fig. 3 is composed of localities 5, 7, 9, 10, 8, and 6; it represents animals from western Oklahoma. Animals from the easternmost localities (1, 2, 3) cluster to the left. *D. ordii* from locality 4 appear intermediate between the two main clusters. The minimally connected network shows animals within one major cluster to be most similar to animals from localities within that cluster. Specimens from locality 3 are linked to *D. ordii* at locality 5 through specimens from locality 4. In general, kangaroo rats from localities 1 through 8 grouped according to their geographic location along the South Canadian River (Fig. 3). Only specimens from locality 6, the largest *D. ordii* examined, appear to be out of place and group with other western localities. Specimens from localities 9 and 10, although not from the South Canadian River floodplain, are large, group with specimens from other western localities, and are most similar to animals from locality 7 (Fig. 3). Arrangement of specimens geographically is also shown by the discriminant classification function scores presented in Table 4. These results

TABLE 4.—*Predictions of group membership based on discriminant classification function scores for* Dipodomys ordii *from 10 localities along the South Canadian River in Oklahoma. Specimens from localities 2 and 9 were used as end groups and* D. ordii *from other localities were tested for membership in locality 2 or 9 in order to determine which of the end groups individuals were most similar to based on 12 morphologic characters. See Fig. 1 for explanation of localities.*

Locality	N	Group 2		Group 9	
		Assigned individuals	Percent	Assigned individuals	Percent
1	3	1	33.33	2	66.67
2	22	20	90.91	2	9.09
3	29	22	75.86	7	24.14
4	14	10	71.43	4	28.57
5	13	4	30.77	9	69.23
6	13	2	15.38	11	84.62
7	25	7	28.00	18	72.00
8	28	3	10.71	25	89.29
9	33	1	3.03	32	96.97
10	9	0	0.00	9	100.00

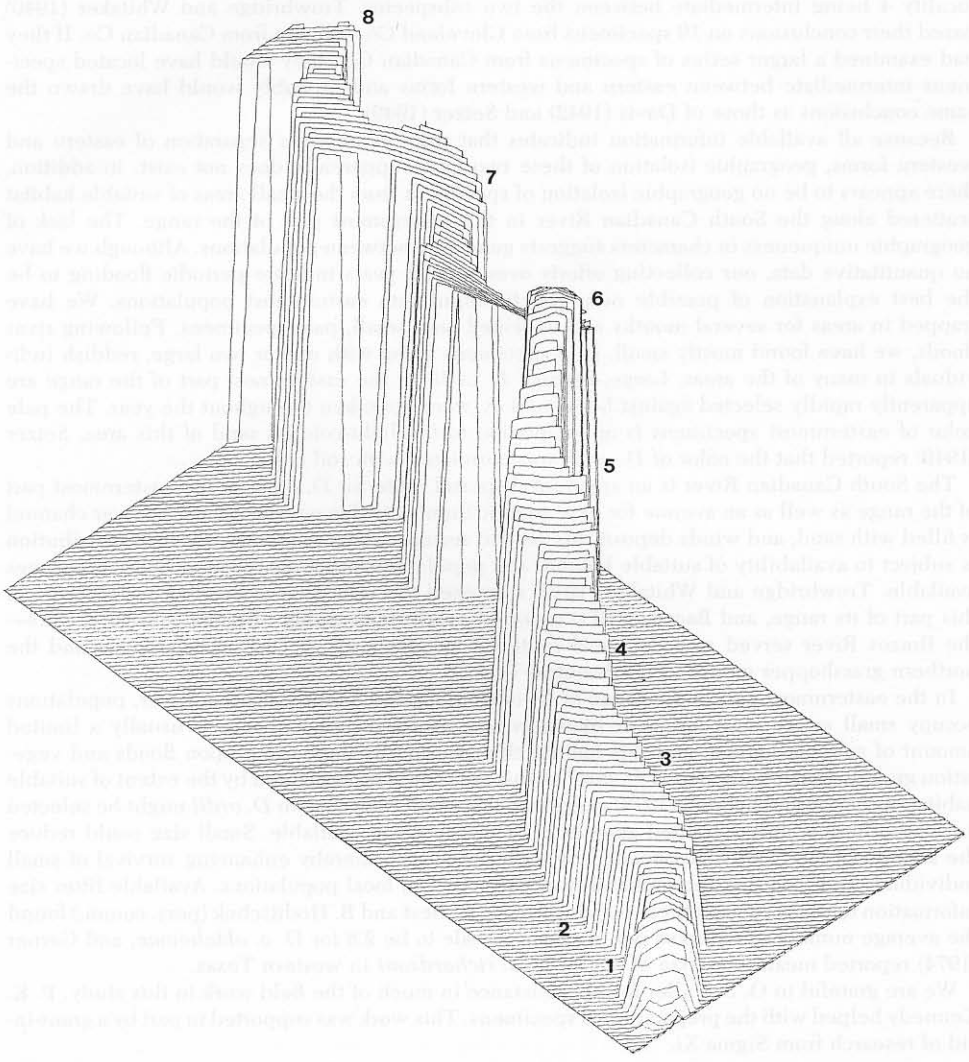

FIG. 4.—A three-dimensional line-drawing illustrating absolute values of projections on component I (size variation) for 12 skull characters of *Dipodomys ordii*. Locality numbers 1–8 (see Fig. 1 for locality numbers) have been placed in approximate position along the drawing for clarity.

emphasize the gradual intergradation between eastern and western forms. All localities sampled contained specimens characteristic of both end groups (localities 2 and 9). However, localities 2 through 4 have a high percentage of specimens with membership in group 2 whereas localities 5 through 10 contain a high percentage of specimens similar to those taken from locality 9. The only eastern locality with a higher percentage of specimens with membership in group 9 is locality 1, but only three specimens composed this sample and small sample size may be responsible for this contradiction.

Our results support Davis' (1942) conclusion that the two Oklahoman forms of kangaroo rats differ only in the average of characters. We found no clear separation between these forms but rather a gradation of large specimens (*D. o. richardsoni*) from western localities (5, 7, 9, 10, 8, 6) to smaller specimens (*D. o. oklahomae*) in more eastern localities (1, 2, 3) with specimens at

locality 4 being intermediate between the two subspecies. Trowbridge and Whitaker (1940) based their conclusions on 19 specimens from Cleveland Co. and one from Canadian Co. If they had examined a larger series of specimens from Canadian Co., they would have located specimens intermediate between eastern and western forms and probably would have drawn the same conclusions as those of Davis (1942) and Setzer (1949).

Because all available information indicates that there is no clear separation of eastern and western forms, geographic isolation of these two forms apparently does not exist; in addition, there appears to be no geographic isolation of specimens from the small areas of suitable habitat scattered along the South Canadian River in the easternmost part of the range. The lack of geographic uniqueness in characters suggests gene flow between populations. Although we have no quantitative data, our collecting efforts over several years indicate periodic flooding to be the best explanation of possible new genetic input into easternmost populations. We have trapped in areas for several months and collected only small, pale specimens. Following river floods, we have found mostly small, pale specimens along with one or two large, reddish individuals in many of the areas. Large, reddish *D. ordii* in the easternmost part of the range are apparently rapidly selected against because they were not taken throughout the year. The pale color of easternmost specimens is an adaptation to the light-colored sand of this area. Setzer (1949) reported that the color of *D. ordii* was correlated with soil color.

The South Canadian River is an apparent dispersal route for *D. ordii* in the easternmost part of the range as well as an avenue for new genetic input into this eastern area. The river channel is filled with sand, and winds deposit this sand as terraces along the banks. *D. ordii* distribution is subject to availability of suitable habitat, and populations move eastward as habitat becomes available. Trowbridge and Whitaker (1940) discussed the influence of flooding on *D. ordii* in this part of its range, and Baccus (1971) reported results concerning dispersal similar to ours—the Brazos River served as a dispersal route for species such as Ord's kangaroo rat and the northern grasshopper mouse in northcentral Texas.

In the easternmost part of the range of *D. ordii* along the South Canadian River, populations occupy small active sand dunes or blowouts on stabilized dunes. There is usually a limited amount of suitable habitat, and this habitat changes rapidly depending upon floods and vegetation growth. Small body size of *D. ordii* in this area could be explained by the extent of suitable habitat. Kennedy and Schnell (1978) suggested that small body size in *D. ordii* might be selected for when there is only a limited amount of desirable space available. Small size could reduce the amount of food and space needed by each individual, thereby enhancing survival of small individuals and lowering the probability of extinction in local populations. Available litter size information tends to support these conclusions. T. L. Best and B. Hoditschek (pers. comm.) found the average number of embryos per pregnant female to be 2.8 for *D. o. oklahomae,* and Garner (1974) reported mean litter size of 2.5 for *D. o. richardsoni* in western Texas.

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