

INTRASPECIFIC VARIATION IN THE AGILE KANGAROO RAT (*DIPodomys AGILIS*)

TROY L. BEST

ABSTRACT.—Intraspecific variation in external and cranial measurements of agile kangaroo rats (*Dipodomys agilis*) was evaluated using 3,078 adult specimens (1,694 males and 1,384 females). Males were larger than females for 17 of 19 characters examined, and significant geographic variation occurred in all characters for both sexes. Larger individuals were found in the northern and southern extremes of the species' range, and the smallest were in northern Baja California. Populations represented mostly by *D. a. perplexus* and *D. a. fuscus* tended to group separately from the others in some of the analyses, but no species-level differences were detected between populations.

The agile kangaroo rat (*Dipodomys agilis*) occurs from Tulare Co., California, southward across the Magdalena Plain of Baja California, and westward to the Pacific Ocean. Populations near Lompoc, Santa Barbara Co., California, and on the Magdalena Plain of southern Baja California are not contiguous with those of the rest of the species. Several authors (for example, Grinnell, 1922, 1933; Huey, 1927, 1951; Vaughan, 1954; Lackey, 1967) have described the diverse habitats occupied by *D. agilis*, from the Pacific Coast to the top of the Sierra San Pedro Martir and from the dense chaparral of southern California to the sparsely vegetated Magdalena Plain.

Huey (1951: 245) considered the southern populations of *D. agilis* to be a distinct species and referred them to *D. peninsularis* because of "Certain basic characters . . . such as extremely inflated bullae, brightly colored and heavily boned tail and average dorsal color tones . . ." Additionally, he described *D. paralius* (Huey, 1951) and *D. antiquarius* (Huey, 1962) from Santa Catarina Landing and San Juan Mine, Sierra San Borja, respectively. Lackey (1967) examined these species and concluded that *D. antiquarius* should be placed into the same group as *D. agilis*, not with *D. stephensi* as Huey (1962) proposed, and that *D. antiquarius* had a close relationship with *D. peninsularis*. Stock (1974) reported identical karyotypes for *D. agilis simulans*, *D. a. plectilis*, and *D. peninsularis pedionomus*, and speculated that they might be conspecific with *D. paralius* and *D. antiquarius*. I (Best, 1978, 1981a) examined morphologic variation in 13 populations of the *heermanni* group of kangaroo rats in Baja California, including *D. agilis*, *D. peninsularis*, *D. paralius*, *D. antiquarius*, and *D. gravipes*. My analyses indicated that these forms represented only two species—*D. agilis* and *D. gravipes*.

Chromosomal polytypy within *Dipodomys* occurs in *D. panamintinus*, *D. agilis*, *D. spectabilis* (Stock, 1974), and *D. microps* (Csuti, 1979). Stock (1974) noted that the karyotype of *D. a. perplexus* (2N = 62; FN = 110) differed from the subspecies *simulans*, *plectilis*, and *pedionomus* (2N = 60; FN = 116). Csuti (1971) had previously found 2N = 62 and FN = 116 for *D. a. agilis* and *D. a. perplexus*. They (Csuti, 1971; Stock, 1974) examined 50 *D. agilis* from nine localities; specimens from California had 2N = 62 and those from Baja California had 2N = 60.

Considering the diversity of habitats occupied by *D. agilis* and the chromosomal polytypy, it is possible that species-level differences exist between the northern and southern populations of *D. agilis*. This would be a pattern similar to that proposed by Huey (1951), but the separation would be much farther north. To determine if populations of *D. agilis* differ between areas, I studied morphologic variation of specimens collected throughout its range. My purposes were to investigate the degree of sexual dimorphism, amount and pattern of interlocality variation within each character, phenetic relationships among populations, and species-level relationships of populations.

MATERIALS AND METHODS

A total of 4,394 *D. agilis* was examined. I analyzed five external and 14 cranial measurements for the 3,078 adult specimens with adequate collection locality data (1,694 males from 501 localities and 1,384

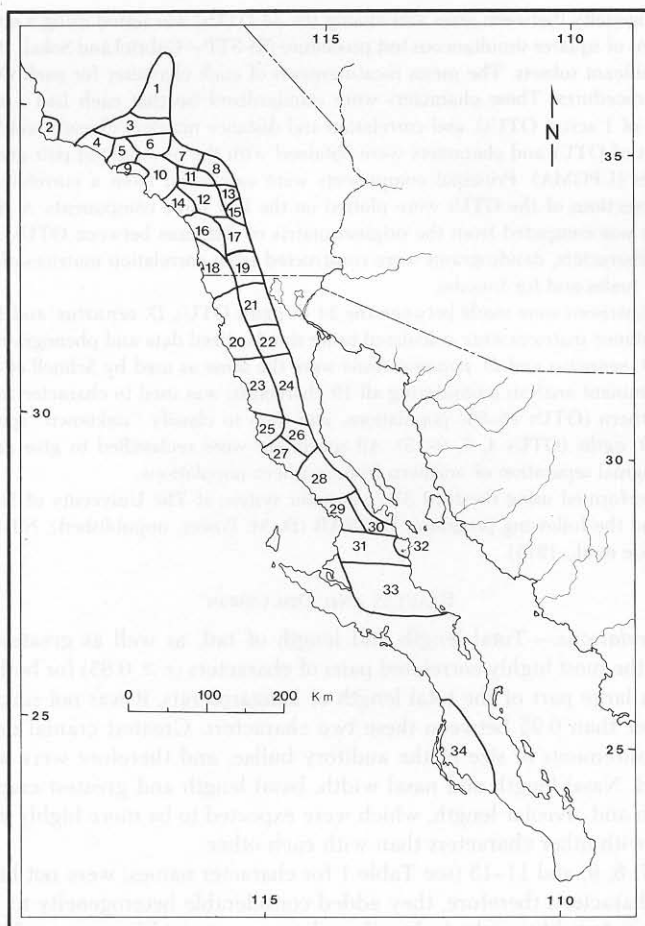


FIG. 1.—Distribution of the agile kangaroo rat (*Dipodomys agilis*) in California and Baja California. The numbers refer to the groups of localities analyzed (OTUs). The code name and sample size for each OTU are given in the text.

females from 434 localities). The 19 characters used were described previously (Best, 1978). External characters were recorded to the nearest mm from the specimen tag, and cranial measurements were made to the nearest 0.1 mm using dial calipers. Specimens were aged according to the cranial criteria of Best and Schnell (1974).

Localities were plotted onto U.S. Geological Survey maps (1:250,000) of California and the maps of Baja California in Gerhard and Gulick (1967). Then localities were grouped into 34 Operational Taxonomic Units (OTUs) giving consideration to geographic features, previous taxonomic designations (Hall, 1981), and habitat differences (Fig. 1). The code name and sample size for each group (OTU) are as follows: 1) S.NEVADA (53 males, 46 females); 2) LOMPOC (8, 3); 3) MT.PINOS (56, 46); 4) STA.YNEZ (19, 9); 5) ST.CLARA (10, 16); 6) MINTCANY (53, 57); 7) SGABRIEL (33, 24); 8) SBERNARD (11, 16); 9) STMONICA (34, 21); 10) FERNANDO (62, 52); 11) RECHECAN (108, 80); 12) RIVERSID (112, 89); 13) BANNING (83, 82); 14) STA.ANA (30, 11); 15) SJACINTO (13, 8); 16) SLUISREY (151, 95); 17) WARNERSP (43, 31); 18) SANDIEGO (99, 70); 19) JACUMBA (51, 38); 20) ENSENADA (47, 41); 21) S.JUAREZ (61, 53); 22) TRINIDAD (135, 148); 23) SQUINTIN (63, 51); 24) SANPEDRO (31, 23); 25) ELROSARI (41, 35); 26) SAGUSTIN (64, 37); 27) CATARINA (14, 16); 28) CHAPALA (38, 34); 29) ROSARITO (19, 12); 30) SANBORJA (11, 5); 31) ELARCO (57, 55); 32) S.FRANCI (11, 5); 33) SIGNACIO (33, 31); 34) MAGDALEN (33, 37).

Character heterogeneity (between sexes and among the 34 OTUs) was tested using a one-way analysis of variance, and a sums of squares simultaneous test procedure (SS-STP—Gabriel and Sokal, 1969) to determine maximally nonsignificant subsets. The mean measurements of each character for each OTU were used in the multivariate procedures. These characters were standardized (so that each had a mean of 0 and a standard deviation of 1 across OTUs), and correlation and distance matrices (Sneath and Sokal, 1973) were calculated. Clusters of OTUs 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 OTUs were plotted on the first three components. A shortest minimally connected network was computed from the original matrix of distances between OTUs. To elucidate correlations between characters, dendrograms were constructed from correlation matrices of the 19 standardized characters for males and for females.

Interspecific comparisons were made between the 34 *D. agilis* OTUs, *D. venustus*, and *D. panamintinus*. Correlation and distance matrices were calculated using standardized data and phenograms were constructed. The data for *D. venustus* and *D. panamintinus* were the same as used by Schnell et al. (1978).

Canonical discriminant analysis (considering all 19 characters) was used to characterize northern (OTUs 1–3, 6–8) and southern (OTUs 16–34) populations, and then to classify “unknown” specimens from the central range of *D. agilis* (OTUs 4, 5, 9–15). All specimens were reclassified to give an estimate of the accuracy of the original separation of northern from southern populations.

Analyses were performed using the IBM 370 computer system at The University of New Mexico Computation Center and the following programs: UNIVAR (D. M. Power, unpublished), NT-SYS (Rohlf et al., 1972), and SPSS (Nie et al., 1975).

RESULTS AND DISCUSSION

Character correlations.—Total length and length of tail, as well as greatest cranial depth and width, were the most highly correlated pairs of characters ($r \geq 0.85$) for both sexes. Because length of tail is a large part of the total length of kangaroo rats, it was not surprising to find a correlation greater than 0.95 between these two characters. Greatest cranial depth and width are the two measurements of size of the auditory bullae, and therefore were also expected to be closely related. Nasal length and nasal width, basal length and greatest cranial length, and interorbital width and alveolar length, which were expected to be more highly correlated, were correlated more with other characters than with each other.

Characters 5, 7, 8, 9, and 11–15 (see Table 1 for character names) were not highly correlated with any other characters; therefore, they added considerable heterogeneity to the data set for males and females. In addition, body length and zygomatic width were not highly correlated with any of the other characters for females. This character set is more heterogeneous than the ones of Kennedy and Schnell (1978) for *D. ordii* and Best (1978) for *D. agilis*–*D. gravipes*. Because of the relatively low correlations, each character contributed useful information.

Sexual dimorphism.—Grinnell (1922: 90) thought the sexes of *D. a. agilis* “. . . to be practically identical as regards both size and proportions of the skull.” I found that length of ear and the 14 cranial characters were less than 0.5 mm greater in size for males than females; total length (4.9 mm difference between sexes), length of body (2.0 mm), length of tail (2.8 mm), and length of hind foot (0.5 mm) were also greater for males. Analyses of the 19 morphologic characters revealed that 17 exhibited significant secondary sexual dimorphism in size. Two characters (alveolar length and lacrimal length) were not significantly different between sexes. Of the morphologic characters, all except maxillary arch spread ($P < 0.01$) were significant at $P < 0.001$.

Data for *D. ordii* (Kennedy and Schnell, 1978), *D. compactus* (Schmidly and Hendricks, 1976; Baumgardner and Schmidly, 1981), *D. merriami* (Lidicker, 1960), *D. gravipes* (Best, 1983), *D. phillipsii* (Genoways and Jones, 1971), *D. spectabilis* (Nader, 1978), *D. deserti* (Nader, 1978), and *D. microps* (Csuti, 1979) indicate fewer secondary sexually dimorphic characters in other kangaroo rats than for *D. agilis*. Considering the small absolute differences between the means of measurements for male and female *D. agilis*, a large sample is probably necessary to detect the dimorphism.

Interlocality character variation.—Significant interlocality heterogeneity was shown by all

TABLE 1.—Character loadings¹ of the first three principal components of interOTU phenetic variation among 19 characters of the agile kangaroo rat (*Dipodomys agilis*).

Character	Char. no.	Sex	Principal components		
			I	II	III
External					
Total length	1	♂♂	0.883	−0.393	0.047
		♀♀	0.850	−0.418	0.092
Body length	2	♂♂	0.876	−0.094	0.049
		♀♀	0.762	0.056	0.155
Tail length	3	♂♂	0.785	−0.492	0.062
		♀♀	0.738	−0.557	0.050
Hind foot length	4	♂♂	0.912	−0.093	−0.002
		♀♀	0.926	−0.199	−0.023
Ear length	5	♂♂	0.668	−0.480	0.236
		♀♀	0.641	−0.518	−0.082
Cranium					
Basal length	6	♂♂	0.905	−0.359	0.041
		♀♀	0.881	−0.352	−0.086
Greatest length	7	♂♂	0.903	0.281	0.039
		♀♀	0.879	0.311	0.176
Maxillary arch spread	8	♂♂	0.842	0.277	0.004
		♀♀	0.860	0.231	−0.265
Interorbital width	9	♂♂	0.117	0.322	0.805
		♀♀	0.034	0.718	0.344
Nasal width	10	♂♂	0.885	−0.255	0.143
		♀♀	0.868	−0.281	0.197
Intermaxillary width	11	♂♂	0.540	0.664	0.160
		♀♀	0.671	0.593	0.155
Alveolar length	12	♂♂	0.307	0.393	0.293
		♀♀	0.279	0.559	−0.368
Lacrimal length	13	♂♂	0.685	0.263	−0.447
		♀♀	0.597	0.278	−0.629
Maxillary arch width	14	♂♂	0.439	0.514	−0.403
		♀♀	0.516	0.649	0.215
Basioccipital length	15	♂♂	0.457	0.248	−0.202
		♀♀	0.510	−0.078	0.615
Greatest depth	16	♂♂	0.530	0.718	0.215
		♀♀	0.422	0.799	0.077
Greatest width	17	♂♂	0.275	0.885	0.209
		♀♀	0.303	0.892	0.183
Zygomatic width	18	♂♂	0.933	0.032	−0.027
		♀♀	0.872	0.071	−0.192
Nasal width	19	♂♂	0.696	−0.583	0.143
		♀♀	0.705	−0.547	0.064
Total ²		♂♂	50.26	19.62	7.16
		♀♀	47.87	24.05	7.20

¹ Correlations of OTU mean values of individual characters with the component axes.² Percent of total phenetic variance explained.

characters for both sexes ($P \leq 0.001$). As evidenced by the F -ratios for both sexes, body length, interorbital width, alveolar length, lacrimal length, maxillary arch spread, and basioccipital length exhibited the least interlocality variation (F -ratio < 8), whereas length of hind foot, basal length of cranium, and greatest width of cranium exhibited the greatest (F -ratio > 20).

The F -ratios for each character were approximately the same for each sex, but males had

slightly higher values for characters 1, 3, 5–7, 10–12, and 16–19, indicating that they had a greater degree of interlocality variation. When *D. agilis* were analyzed with *D. gravipes* (Best, 1978) the extent of interlocality variation was different for males and females for a number of characters. For *D. ordii*, Kennedy and Schnell (1978) found females to have slightly higher *F*-ratios for most characters.

In both sexes the largest individuals for most of the 19 characters were in the northern and southern populations, intermediate-sized animals occurred toward the middle of the species' range, and the smallest specimens were in north-central Baja California. For males, the largest population means for most characters were for OTUs 1–8, 11, 19, 25, and 30–34; the smallest were for 12, 16, 18, 20, 23, 24, 27, and 28. For females, OTUs 1–4, 6–9, 15, 17, 19, 21, and 28–34 generally had larger means for each character and 12, 16, 18, 20, 23, and 24 were the smallest.

OTUs 1–3 and 6–8 were rather consistently the largest for most characters and were generally larger than the populations in the extreme south (OTUs 31, 33, and 34). For length of ear, OTUs 1, 3, and 6–8 were among the longest, and OTU 2 was intermediate to all the OTUs. OTUs 1–3 and 6–8 occasionally fell into the lower means for some characters, e.g., interorbital width, alveolar length, maxillary arch width, basioccipital length, greatest depth, and greatest width. However, these lower means were represented by only a few members of the OTU 1–3 and 6–8 group.

Multivariate analysis.—Phenograms for both sexes, constructed from correlation and distance matrices of the 19 characters, are presented in Fig. 2. Each of the correlation phenograms (Figs. 2A and 2C) can be divided into two primary clusters at a correlation of about -0.25 . In males, the upper cluster contains OTUs 1–18 and 20, and the remaining OTUs compose the second cluster. Similarly for females, OTUs 1–21 make up one cluster and the remaining OTUs make up the other. The only major difference between the sexes is the inclusion of OTUs 19 and 21 in the female's upper cluster, and their inclusion in the lower cluster for males. These OTUs are adjacent near the U.S.-Mexico border (Fig. 1). OTU 19 is intermediate in size for most characters for both sexes and OTU 21 is intermediate for females and generally smaller for males.

The distance phenograms also show two major clusters for both sexes that appear to generally represent size variation between the OTUs (Figs. 2B and 2D). For males OTUs 1–4, 6–8, 31, and 34 compose one cluster; these represent the seven northernmost and two of the southernmost OTUs (Fig. 1). The lower cluster contains populations with mostly intermediate to small sized individuals. For females, the northernmost OTUs (1–3 and 6–8) form a cluster (Fig. 1). The second major cluster can be separated into two groups; one composed of OTU 25 and the four southernmost OTUs and the other with the remaining 22 OTUs.

The loadings of characters on the first three component axes are presented in Table 1, and three-dimensional (3-D) projections are depicted in Fig. 3. The character correlations with principal component I for both males and females are high for all characters except interorbital width, alveolar length, and greatest width of cranium. Following the reasoning of Johnston and Selander (1971), Niles (1973), Kennedy and Schnell (1978), and Best (1981b), this component may be taken to represent overall size in both sexes because it accounts for most of the covariation among characters. For both sexes OTUs 1–3, 6–8, 31, 33, and 34 have the highest loadings along component I (Fig. 3). This component accounts for about one-half of the phenetic variation (Table 1). In males, OTU 4 is also among the largest OTUs. Thus, the larger animals are in the northern and southern extremes of the range of *D. agilis*. OTUs 23, 24, and 27 (from northern Baja California) have among the lowest loadings along component I for males and females.

On principal component II, alveolar length, maxillary arch spread, greatest depth of cranium, and greatest width of cranium have higher loadings than on component I for both sexes (Table 1). Additionally, intermaxillary width for males and interorbital width for females had high loadings on this component, while other characters for both sexes had only weak associations.

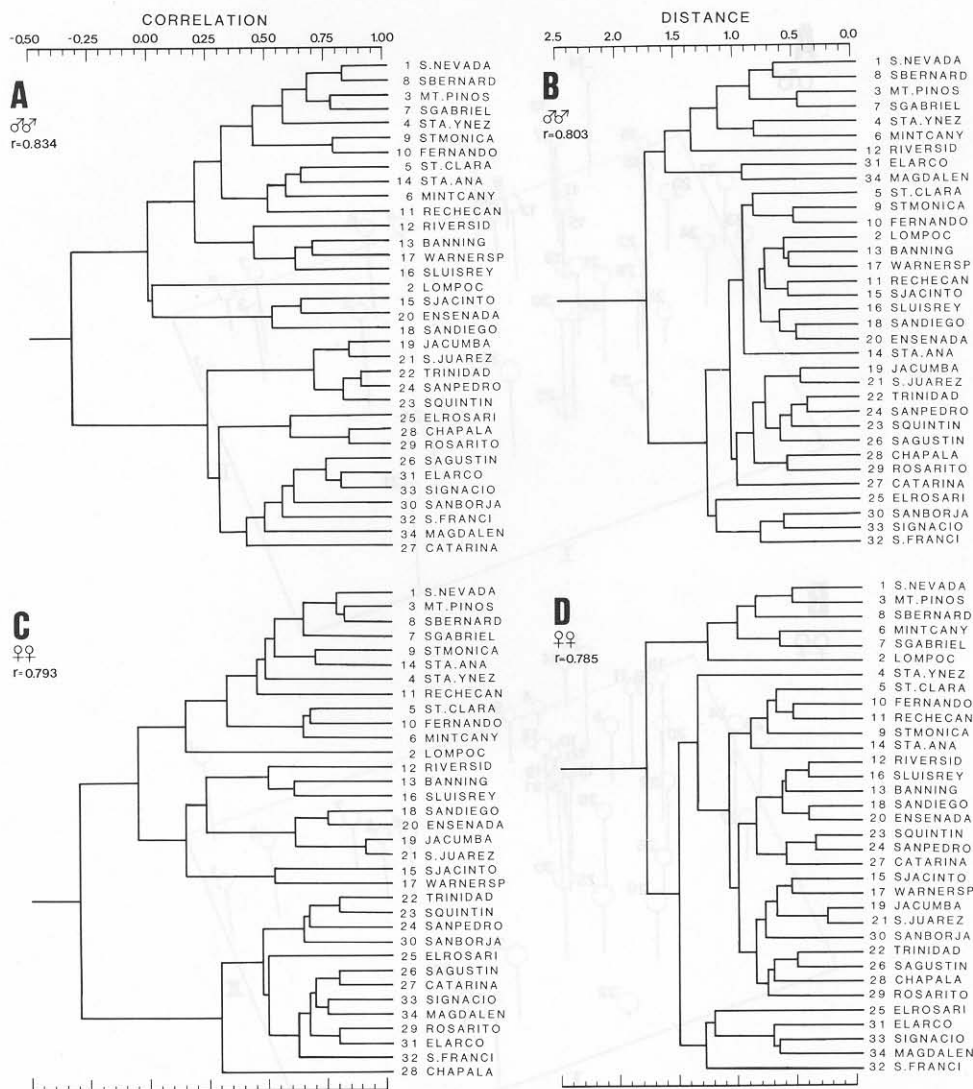


FIG. 2.—Phenograms constructed from correlation and distance matrices for male (A and B, respectively) and female (C and D, respectively) *Dipodomys agilis*. Clusters were obtained using the UPGMA. Accuracy of the diagrams in depicting interOTU relationships increases from left to right. Numerical identifications are the same as in Fig. 1. The cophenetic correlation coefficient (r) is indicated.

The 20% of the variance accounted for by this component for males and the 24% for females (Table 1) is shown in a rather uniform spread of OTUs across the component.

The third principal component for males has highest loadings for interorbital width, lacrimal length, and maxillary arch spread. The females have high loadings for lacrimal length and basioccipital length and much lower loadings for all other characters. Only about 7% of the phenetic variance is explained by this component (Table 1); no particular trends can be detected along this third component (Fig. 3).

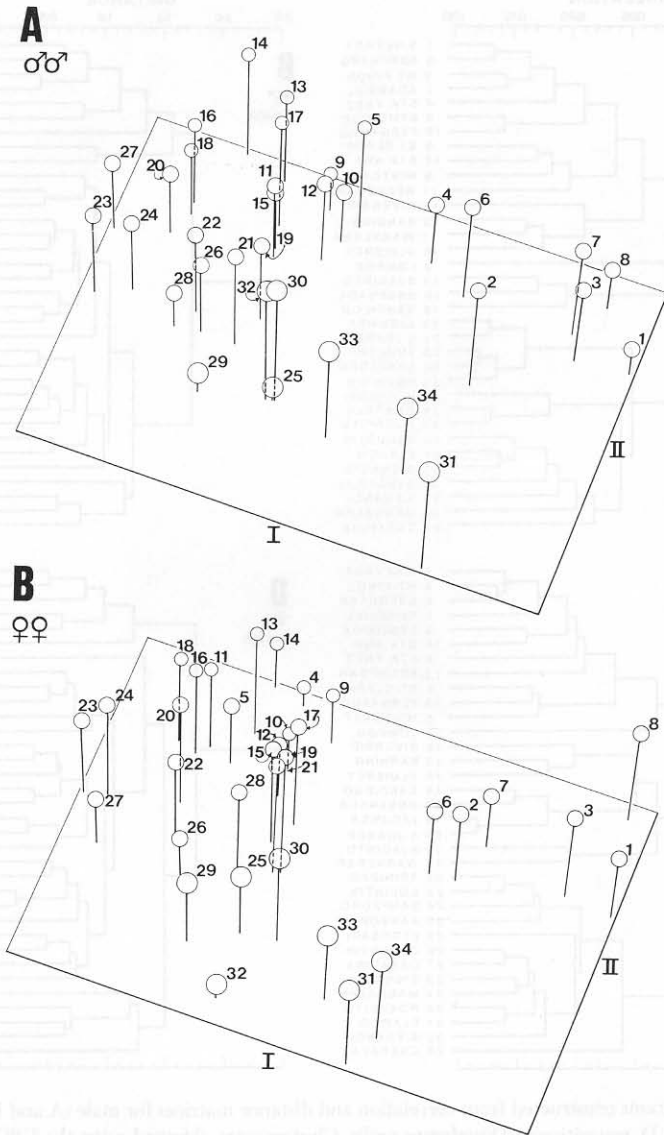


FIG. 3.—Three-dimensional projections of OTUs onto the first three principal component axes of variation in the matrix of correlations of 19 morphologic characters for male (A) and female (B) *Dipodomys agilis*. The shortest simply-connected networks, derived from the matrix of distance coefficients for the same characters are as follows: males, 1-8, 8-7, 7-3, 7-6, 6-5, 5-12, 12-10, 10-9, 12-15, 15-11, 11-17, 17-13, 13-16, 16-18, 18-20, 12-19, 19-21, 19-22, 22-24, 24-23, 22-26, 22-28, 28-29, 23-27, 10-4, 29-25, 26-30, 30-33, 33-32, 17-14, 33-34, 33-31, and 3-2; females, 1-3, 3-8, 3-7, 7-6, 6-17, 17-21, 21-19, 17-15, 21-28, 28-26, 26-22, 22-20, 20-18, 18-16, 16-11, 22-24, 24-23, 23-27, 16-13, 26-29, 18-5, 5-10, 10-12, 10-9, 21-30, 30-33, 33-34, 33-31, 26-25, 9-14, 29-32, 10-4, and 3-2. The numbers correspond to the OTUs shown in Fig. 1.

The three components explain almost 80% of the total character variation for each sex (Table 1). Thus, distortion of the phenetic distances between OTUs is relatively small when the character space is reduced to three dimensions. Previous principal components analyses of variation

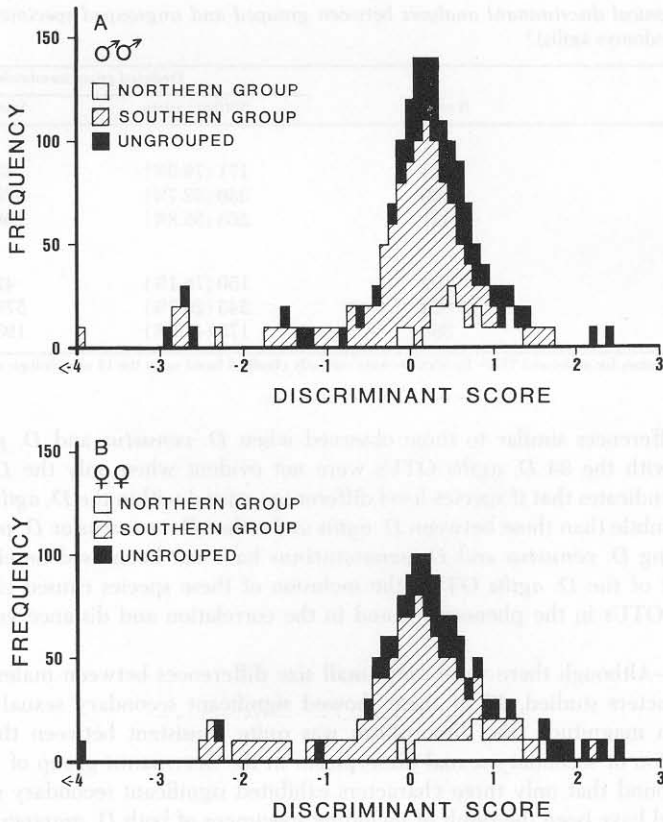


FIG. 4.—Histograms of scores derived from canonical discriminant analysis of male (A) and female (B) *Dipodomys agilis*. The northern group is composed of OTUs 1–3, 6–8, the southern group of OTUs 16–34, and the unknown group of OTUs 4, 5, 9–15.

in *Dipodomys* have explained a greater percent of the total character variation (Best, 1978; Kennedy and Schnell, 1978). This difference is mostly due to the greater percentages of variation represented on principal component I, i.e., 68% by Best (1978) and 70% by Kennedy and Schnell (1978) compared to about 50% herein.

The placement of OTUs 1–3 and 6–8 somewhat distant from the other OTUs in the univariate analyses, dendrograms (Fig. 2), and 3-D plots (Fig. 3) was the basis for the selection of reference populations for discriminant analyses. Histograms depicting the results of the discriminant classification analyses are shown in Fig. 4. For both sexes, discriminant scores among the northern, southern, and unknown groups were very similar. Variability in discriminant scores was greater for males than females, and some specimens had scores falling beyond ± 2 (129 males and 126 females); however, many of these specimens had a large number of characters with missing values. The discriminant analyses showed no clear separation between northern, southern, and unknown samples (Table 2). A large number of individuals from the northern group were placed into the southern group and vice versa for males and females; 70% of males and 72% of females were correctly classified in the analyses.

To verify the degree of differences that might have been shown if species-level variation existed in the *D. agilis*, analyses were performed including *D. venustus* and *D. panamintinus* with the 34 *D. agilis* OTUs. For both sexes, *D. venustus* and *D. panamintinus* clustered among the *D. agilis* OTUs in the correlation phenograms, but were widely separated in the distance

TABLE 2.—Canonical discriminant analyses between grouped and ungrouped specimens of the agile kangaroo rat (*Dipodomys agilis*).¹

Actual group	N cases	Predicted group membership	
		Northern group	Southern group
Males			
Northern group	214	171 (79.9%)	43 (20.1%)
Southern group	1,009	330 (32.7%)	679 (67.3%)
Ungrouped	471	263 (55.8%)	208 (44.2%)
Females			
Northern group	192	150 (78.1%)	42 (21.9%)
Southern group	824	245 (29.7%)	579 (70.3%)
Ungrouped	368	175 (47.6%)	193 (52.4%)

¹ 69.5% of the grouped cases for males and 71.8% for females were correctly classified based upon the 19 morphologic characters.

phenograms. Differences similar to those observed when *D. venustus* and *D. panamintinus* were analyzed with the 34 *D. agilis* OTUs were not evident when only the *D. agilis* were compared. This indicates that if species-level differences existed within the *D. agilis* OTUs, they are much more subtle than those between *D. agilis* and either *D. venustus* or *D. panamintinus*. Analyses including *D. venustus* and *D. panamintinus* have not been used herein to evaluate the arrangement of the *D. agilis* OTUs; the inclusion of these species caused changes in the arrangement of OTUs in the phenograms and in the correlation and distance values between them.

Significance.—Although there were only small size differences between males and females for the 19 characters studied, 17 of these showed significant secondary sexual dimorphism. Though small in magnitude, the dimorphism was quite consistent between the sexes. In a previous evaluation of secondary sexual dimorphism in the *heermanni* group of kangaroo rats (Best, 1978), I found that only three characters exhibited significant secondary sexual dimorphism. This could have been the result of including specimens of both *D. gravipes* and *D. agilis* in the same analyses, which would increase the variance within sexes, or may have been due to the relatively small sample examined. When I analyzed *D. gravipes* separately (Best, 1983) there were three external and four cranial characters that exhibited significant secondary sexual dimorphism.

Univariate and multivariate assessments of the phenetic relationships among the populations of *D. agilis* were similar, i.e., there were larger populations at the northern and southern extremes of the range and smaller ones in the middle. Except for the tendency of OTUs 1–3 and 6–8 to appear together, there were no clear separations of populations in any of the SS-STP analyses, dendrograms, three-dimensional plots, or discriminant analyses. All analyses indicated no morphologic separation of populations into units that could be considered as specifically distinct. In addition, there seemed to be no distinct separation of *D. a. fuscus* (OTU 2) from *D. a. perplexus* (OTUs 1, 3, 6–8) in the analyses.

The chromosomal differences reported by Csuti (1971) and Stock (1974) were not strongly reflected in the morphologic differences between the populations. However, it is interesting that the localities in California where Csuti and Stock collected specimens for karyotyping were very close to the OTUs that showed the greatest separation among those studied herein (1–3 and 6–8). Csuti's specimens from the Mt. Piños area were from my OTU 3, those from near Los Angeles were from OTU 10, and Stock's specimens were from OTU 11. The only other published karyotypes of *D. agilis* were from Baja California specimens occurring in my OTUs 23, 25, and 26 (Stock, 1974). Thus, there may be chromosomal differences associated with some of the morphologic variation, but there is a paucity of specimens with karyotypic data, especially from Los Angeles southward to near San Quintin and south of San Agustin. Further studies are needed to elucidate the extent of the karyotypic variation and to investigate the relationship of that variation with differences in morphologic traits over the range of *D. agilis*.

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Department of Biology and Museum of Southwestern Biology, The University of New Mexico, Albuquerque, NM 87131. Submitted 20 September 1982. Accepted 24 February 1983.