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Relationships between Ecogeographic and Morphologic Variation of the Agile Kangaroo Rat (*Dipodomys agilis*) in Baja California, Mexico

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Abstract.—Relationships between ecogeographic and morphologic variation of the agile kangaroo rat (*Dipodomys agilis*) in Baja California, Mexico by Troy L. Best, *Bull. Southern California Acad. Sci.,* 80(2):60–69, 1981. Interlocality variation in temperature and precipitation were analyzed for 11 localities in Baja California where kangaroo rats (*Dipodomys agilis*) were collected. Correlations between these data and kangaroo rat morphologic variation were determined. Principal component I (size) of the morphologic data was significantly correlated with latitude and longitude for both sexes. The female component II (nasal width, ulna length, and hind foot length) was correlated with July mean temperature and January mean precipitation.

Previously I examined external, skeletal, bacular, and burrow variation in populations of kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico (Best 1978, 1981, 1982). The present study examines intraspecific morphologic variation and its covariation with ecogeographic parameters for one species of the group, *Dipodomys agilis*.

In their review of geographic variation studies, Gould and Johnston (1972) emphasized the importance of examining environmental correlates of geographic variation in populations. Since vertebrate populations are influenced by numerous environmental attributes simultaneously, analyses of general morphologic variation should include comparisons with generalized ecogeographic variation, rather than only to variables measured at each collecting site. Principal components analyses have been used herein to reveal general trends in the multi-character data sets for morphology, temperature, and precipitation. I have examined interlocality variation, and have determined the covariation of ecogeographic variables with morphologic variation. In addition, characters measured at each collection site have been compared to morphologic variation.

Methods

The 216 *D. agilis* collected for this study were from 11 localities in Baja California (Fig. 1). Table 1 lists the 19 morphologic characters examined; sample sizes and descriptions of these characters were given previously (Best 1978). The character numbers and mean values were taken from Best (1976, Appendix I). No female data were obtained for populations 2 and 8. The environmental phenograms and three-dimensional models utilize matrices and phenograms with all 11 localities represented; comparisons involving female matrices were based on 9.

For each locality, altitude, latitude, longitude, temperature, and precipitation were taken from the nearest weather station as determined from the maps in

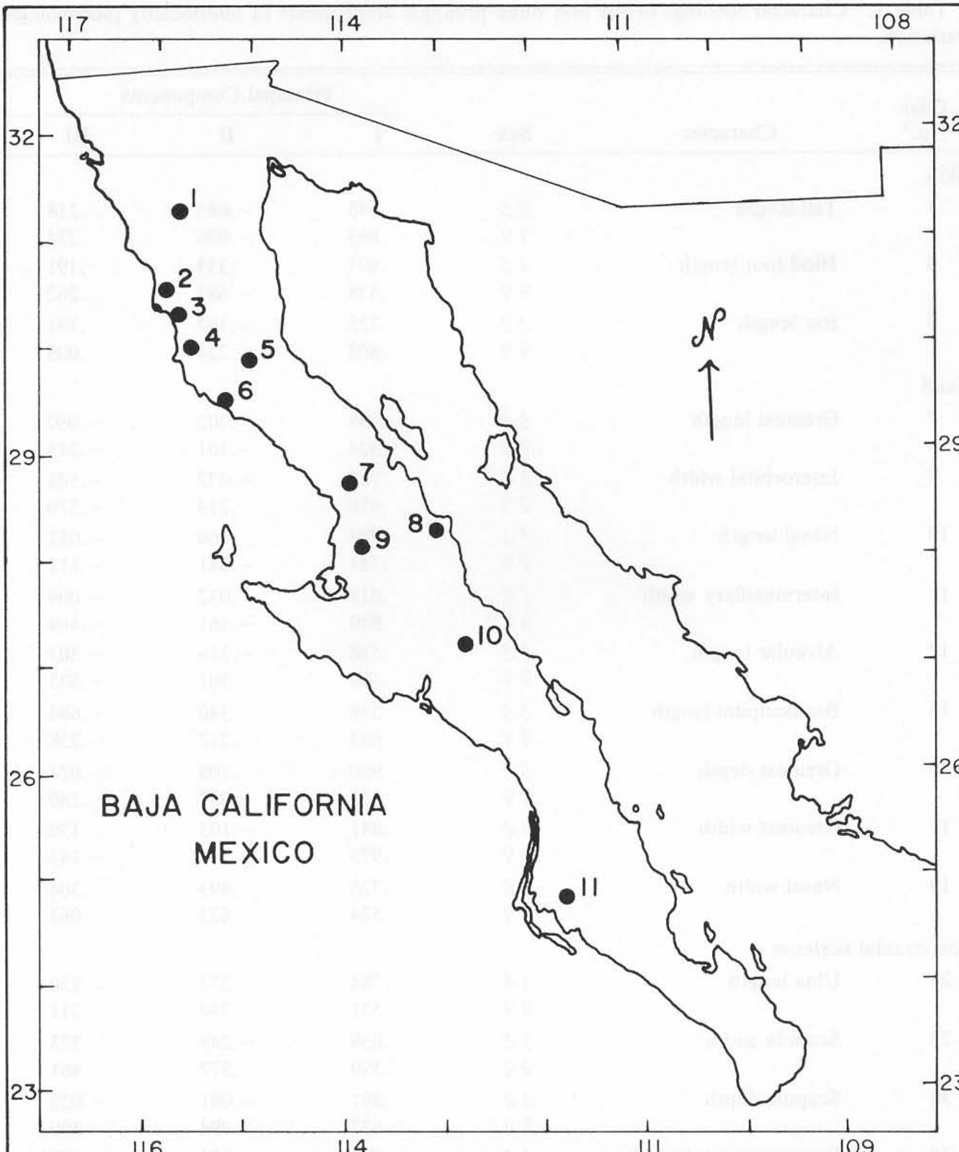

Fig. 1. Map of the 11 localities in Baja California, Mexico, where kangaroo rats (*Dipodomys agilis*) used in this study were collected. Numeral identifications, code names, nearest weather station (from Hastings and Humphrey, 1969), elevations, latitudes, and longitudes are: 1) TRINIDAD Valle de la Trinidad, 900 m, 31°10′30″N, 115°46′30″W; 2) ESCOAGIL Las Escobas, 24 m, 30°20′30″, 115°53′30″; 3) SOCORRO El Socorro, 10 m, 30°20′00″, 115°49′00″; 4) ROSAAGIL El Rosario, 15 m, 30°00′30″, 115°43′30″; 5) AGUSTINE San Agustine, 580 m, 29°50′30″, 115°00′00″; 6) CATARINA Santa Catarina (Sur), 450 m, 29°40′30″, 115°09′30″; 7) SANBORJA San Borja, 375 m, 28°40′00″, 113°56′00″; 8) EL-BARRIL El Barril, 100 m, 28°10′30″, 112°54′00″; 9) R.ALEGRE Rancho Alegre, 500 m, 28°10′00″, 113°53′00″; 10) IGNACIO San Ignacio, 105 m, 27°10′30″, 112°54′00″; and 11) REFUGIO El Refugio, 29 m, 24°40′30″, 111°45′30″.

Table 1. Character loadings of the first three principal components of interlocality morphologic variation.

Char. No.[1]	Character	Sex	Principal Components I	II	III
Skin					
3	Tail length	♂♂	.548	−.685	.218
		♀♀	.863	−.096	.274
4	Hind foot length	♂♂	.691	.333	.191
		♀♀	.538	−.681	.262
5	Ear length	♂♂	.725	−.167	.391
		♀♀	.803	−.224	.003
Skull					
7	Greatest length	♂♂	.954	.202	−.080
		♀♀	.924	−.161	−.243
9	Interorbital width	♂♂	.702	−.077	−.503
		♀♀	.676	.214	−.570
10	Nasal length	♂♂	.844	.360	−.052
		♀♀	.781	−.541	−.112
11	Intermaxillary width	♂♂	.817	−.032	−.009
		♀♀	.849	−.161	−.469
12	Alveolar length	♂♂	.538	−.316	−.303
		♀♀	.389	.501	−.585
15	Basioccipital length	♂♂	.558	.340	−.684
		♀♀	.653	.212	−.258
16	Greatest depth	♂♂	.950	.108	−.027
		♀♀	.831	−.057	−.289
17	Greatest width	♂♂	.881	−.103	.136
		♀♀	.973	−.114	−.143
19	Nasal width	♂♂	.720	.493	.304
		♀♀	.574	.623	.063
Post-cranial skeleton					
23	Ulna length	♂♂	.784	.277	.250
		♀♀	.531	.754	.211
28	Scapula width	♂♂	.839	−.249	.373
		♀♀	.599	.577	.461
30	Scapula depth	♂♂	.891	−.081	−.022
		♀♀	.637	.094	.309
36	Femur proximal width	♂♂	.894	−.203	.075
		♀♀	.916	.023	.315
38	Pelvis depth	♂♂	.941	−.118	.040
		♀♀	.890	.195	.125
40	Pelvic foramen length	♂♂	.740	−.266	−.563
		♀♀	.728	−.514	−.284
42	Number fused vertebrae	♂♂	−.021	.832	−.053
		♀♀	−.315	−.106	−.833
Percent of total variation explained		♂♂	59.1	11.7	9.0
		♀♀	53.5	14.9	13.3

[1] Character numbers correspond to the 19 selected characters used by Best (1978).

Hastings and Humphrey's (1969) report on the climate of Baja California (see Best 1976, Appendices II and III, for temperature and precipitation means used in this study). For both temperature and precipitation I used 12 monthly and 4 seasonal means (Table 2). With one exception, collecting localities were within 20 km of a weather station. For Santa Catarina Landing, which is located on the west coast, the nearest weather station is approximately 35 km inland at an elevation of 450 m.

Product-moment correlation and average distance matrices (Sneath and Sokal 1973) were calculated from the standardized locality means of the morphologic, temperature, and precipitation data for each site. Clusters of localities from these original matrices were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a matrix of correlations among characters and locality means. Projections of the localities were plotted on the first three principal components. A shortest minimally connected network computed from the original matrix of distance coefficients has been superimposed on these three-dimensional plots to indicate where possible distortion may be present.

Analyses were performed using the IBM 370 computer at the University of Oklahoma Computation Center. Bivariate correlations were determined with a program (BIVAR) written by Power (1967), and multivariate analyses were conducted using the NT-SYS series of programs (Rohlf, Kishpaugh, and Kirk 1972).

Results and Discussion

Interlocality Variation

Figure 2 shows phenograms for male and female morphologic variation constructed from correlation and distance matrices. Male (Fig. 1A) and female (Fig. 2C) correlation phenograms are very different, and do not reflect geographic groupings. In the male distance phenogram (Fig. 2B) populations 9 and 11 form a cluster distinct from the other populations, and for females (Fig. 2D) 5, 7, 9, and 11 are separate from the other populations. These results are in close agreement with my previous study that included measurements for *D. gravipes* (Best 1978), indicating that the inclusion of the second species does not greatly change the results of the analyses.

The temperature correlation phenogram (Fig. 2E) shows two very distinct clusters. This represents a separation of the northern-inland and Gulf of California side of the peninsula (localities 1, 5, 6, 8) from the southern and Pacific side of the peninsula. Temperature data for locality 6 were taken about 35 km inland from the actual collecting site, accounting for its inclusion in the Gulf of California-northern-inland cluster. The distance phenogram (Fig. 2F) shows localities 8, 10, and 11 clustered together and well separated from the other localities. These are in the southern half of the peninsula and have the warmest mean annual temperatures.

Two major clusters comprise the precipitation correlation phenogram (Fig. 2G). Localities in the upper cluster are all of the northern localities, except locality 5. The two major clusters in the distance phenogram (Fig. 2H) reflect the difference in mean annual precipitation of the localities. The cluster containing localities 1 and 9 represents the two sites with the greatest mean annual precipitation. Be-

Table 2. Character loadings of the first three principal components of interlocality temperature and precipitation variation.

Char. No.	Character	Temperature I	II	III	Precipitation I	II	III
1	January mean	.853	−.516	−.004	.658	−.446	.503
2	February mean	.893	−.435	−.080	.973	−.113	.067
3	March mean	.951	−.302	−.002	.931	−.036	.105
4	April mean	.993	−.054	−.061	.729	−.380	−.366
5	May mean	.983	.108	−.122	.527	−.353	−.257
6	June mean	.871	.465	−.150	.728	.177	.338
7	July mean	.808	.584	−.004	.511	.817	.006
8	August mean	.818	.565	.082	.202	.835	−.442
9	September mean	.924	.347	.134	−.334	.864	.104
10	October mean	.994	.057	.063	.227	.747	.167
11	November mean	.933	−.327	.066	.912	.240	.304
12	December mean	.908	−.407	.070	.667	−.038	−.371
13	Winter mean	.892	−.452	−.004	.936	−.161	.030
14	Spring mean	.994	−.081	−.062	.806	−.102	−.295
15	Summer mean	.839	.543	−.024	.228	.869	−.230
16	Fall mean	.993	.050	.099	.169	.865	.201
Percent of total variation explained		84.2	14.6	0.6	43.3	29.9	7.7

cause of its extreme aridity, locality 8 is quite divergent from the others in the lower cluster.

Principal Components

The loadings of morphologic characters on the first three component axes are presented in Table 1 and three-dimensional projections are depicted in figures 3A and 3B. The character correlations with principal component I for males are high for all characters except 3 (tail length), 12 (alveolar length), 15 (basioccipital length), and 42 (number of fused vertebrae). For females the only low loadings were for characters 4 (hind foot length), 12 (alveolar length), 19 (nasal width), 23 (ulna length), and 42 (number of fused vertebrae). This component is taken to represent overall size in both sexes, since it accounts for most of the variation among characters. On principal component II, characters 3 (tail length) and 42 (number of fused vertebrae) have highest loadings for males. Characters 4 (hind foot length), 19 (nasal width), and 23 (ulna length) are highest for females. Component III has highest loadings for character 15 (basioccipital length) for males and 42 (number of fused vertebrae) for females. The three components explain about 80% of the total character variance for each sex (see bottom of Table 1).

Principal component I separates populations in figures 3A and 3B by size. For males, populations 1, 3, and 6 are the smallest and 9 and 11 are the largest. The same is true for females; however, the central populations in the figure are not as distinct as for males. This is due to the missing data for female populations 2 and 8, and to the separation along principal component II. This second component in males generally places the longer tailed forms toward the back of the model.

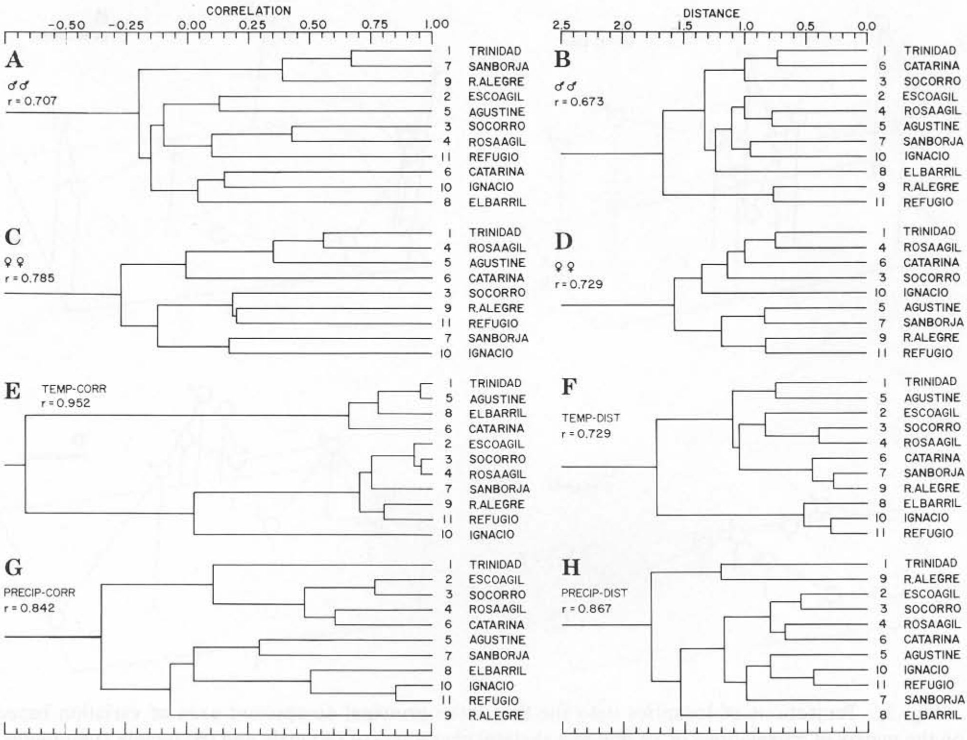

Fig. 2. Phenograms constructed from correlation and distance matrices for: (A and B) male kangaroo rats; (C and D) female kangaroo rats; (E and F) temperature; and (G and H) precipitation in Baja California. Cophenetic correlation coefficients (r) are given; accuracy of the diagrams in depicting interlocality relationships increases from left to right.

For females, populations with shorter hind feet and longer ulnas are in the front of the model. Component III for males separates populations with longer basioccipital lengths from population 2. For females the populations close to the base of the model generally have more fused vertebrae.

Plots of the first three principal components of temperature and precipitation are also presented in Figure 3. All 16 temperature characters for both sexes have high loadings on principal component I (Table 2), which represents 84.2% of the total variance. A listing of the localities from lowest to highest mean annual temperature is as follows: 2, 1, 3, 4, 5, 6, 9, 7, 10, 11, 8 (Best 1976, Appendix II). A similar order appears across the axis representing the first principal component in the 3-D model of temperature variation (Fig. 3C). Principal component II has highest loadings for January, July, August, and summer means. This component represents 14.6% of the total variation, and separates the northern localities into distinct Pacific coastal (2, 3, 4) and inland (1, 5, 6) groupings. As expected, the weather data for locality 5 has placed it more with the inland than coastal sites. Of the southern localities, number 11, representing a Pacific coastal site, is also displaced slightly by this component from the two Gulf of California localities (8 and 10). The third principal component has low loadings for all characters and represents less than one percent of the variation.

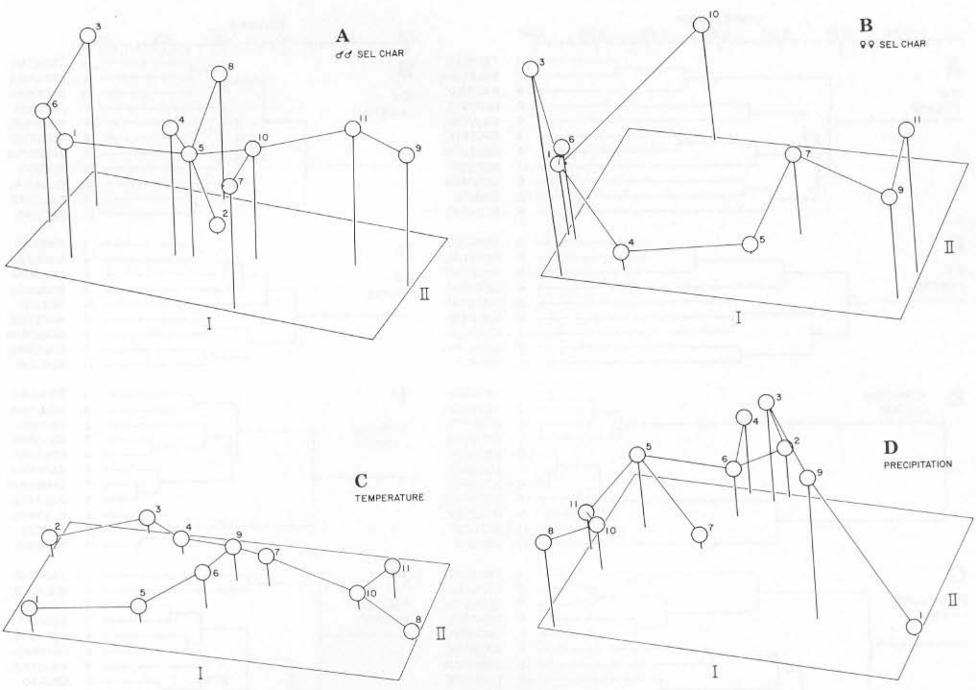

Fig. 3. Projections of localities onto the first three principal component axes of variation based on the matrix of correlations of 19 skin and skeletal characters of (A) male and (B) female *Dipodomys*, (C) 16 temperature characters, and (D) 16 precipitation characters for Baja California. The shortest simply-connected network is superimposed on the principal component space to indicate where possible distortion may be present. Numeral identifications are the same as listed below Figure 1.

Also listed in Table 2 are the results of a principal components analysis of the precipitation data. Figure 3D depicts a plot of these first three components. Principal component I accounts for 43.3% of the variation in the precipitation data. Highest loadings on this component were for the November through May, winter, and spring means. The high character loadings for winter means on component I is shown in the separation of localities along the first axis. Localities on the left have the least winter rainfall and those on the right the greatest. The second component of precipitation variation represents a relatively high percentage of the variation in the data (29.9%). Highest loadings are for July through October, summer, and fall means. Along principal component II the placement of localities 2 through 7 toward the back of the plot, 9, 10, and 11 in the middle, and 1 and 8 at the front appears to be primarily attributable to the summer mean data although the same general grouping of the localities is shown in the fall means (Best 1976, Appendix III).

Hastings and Turner (1965) found the Pacific side of the peninsula received its maximum precipitation in winter, and the Gulf of California side received most of its annual moisture during late summer and fall. These data closely agree with my principal components I and II, representing winter–spring and summer–fall precipitation means, respectively. The third component represents 7.7% of the

Table 3. Product-moment correlation coefficients calculated between the first three principal components of morphologic variation and 11 ecogeographic variables.[1]

Variable	Sex	Principal Components I	II	III
Latitude	♂♂	−.698*	.238	−.232
	♀♀	−.729*	.392	−.314
Longitude	♂♂	−.655*	.250	−.255
	♀♀	−.731*	.530	−.268
Altitude	♂♂	−.137	.586	.026
	♀♀	−.110	.063	−.429
Temperature—January mean	♂♂	.475	−.353	.453
	♀♀	.484	−.282	.441
Temperature—July mean	♂♂	.201	−.133	.247
	♀♀	.326	−.715*	−.154
Temperature—Principal Component I	♂♂	.453	−.325	.374
	♀♀	.594	−.589	.242
Temperature—Principal Component II	♂♂	−.219	.203	−.181
	♀♀	−.179	−.258	−.393
Precipitation—January mean	♂♂	−.109	.052	.086
	♀♀	−.113	.715*	.346
Precipitation—July mean	♂♂	.357	.146	.155
	♀♀	.218	−.190	.055
Precipitation—Principal Component I	♂♂	−.198	.401	−.066
	♀♀	−.283	.421	−.029
Precipitation—Principal Component II	♂♂	.358	−.133	.246
	♀♀	.409	−.431	.015

[1] For values marked (*) r is significant at $P < 0.05$.

variation with the highest loading for the January mean. No general relationship can be detected concerning the distribution of localities along component III.

Environmental-Morphologic Covariation

Results of analyses of covariation of the first three principal components of 19 morphologic characters of Baja California *D. agilis* with 11 ecogeographic variables are presented in Table 3. The first principal component of male and female *Dipodomys* variation is correlated significantly with latitude and longitude. In Kennedy and Schnell's (1978) analyses of 16 cranial characters for *D. ordii*, latitude, mean annual and January temperatures, and mean annual precipitation were significantly correlated with their males' principal component I (size). Latitude, annual, and January mean temperatures were significantly correlated with their female component I (size). Similar results were expected for *D. agilis* in Baja California, since species of *Dipodomys* are morphologically quite similar (Schnell et al. 1978). My data show that body size increases as latitude and longitude decrease (larger animals are in the southern populations). Geographically Baja California juts irregularly from near the United States border, near

32°31′N latitude, southeast across the Tropic of Cancer to Cabo San Lucas, near 22°50′N. This southeastward projection accounts not only for the latitudinal variation, but also for the longitudinal variation. Latitude is very significantly correlated with longitude (r = 0.950, $P < 0.01$) in Baja California. It is clear that the high correlation with longitude does not represent east-west variation across the peninsula, but simply is a result of changing latitude.

Male component II is not correlated with any of the ecogeographic variables, but principal component II for females is significantly correlated with July mean temperature and January mean precipitation (Table 3). These data for females show that southern populations, i.e., those with wider nasal bones, longer ulnas, and shorter hind feet, occur in association with high mean July temperatures and low January mean precipitation.

Principal component III of *Dipodomys* morphologic variation is not significantly correlated with any of the ecogeographic variables. For males, the only character with a high loading for this component was basioccipital length, and for females, number of fused vertebrae in the pelvic girdle (Table 1).

Conclusions

The analyses of environmental variables reported herein elucidate general trends in temperature and precipitation variation in Baja California. The northern region of the peninsula is cooler and receives most of its precipitation during the winter and spring. The warmer southern area has most of its rainfall occurring during the summer and fall. Both sexes of kangaroo rats are generally larger in the southern region of the peninsula; the males have longer tails and more fused vertebrae, and the females have wider nasal bones, longer ulnas, and shorter hind feet. The statistically significant relationships I found cannot be interpreted as cause-and-effect, but they do give an indication of the complex interrelationships of variables that likely interact with vertebrate populations in desert environments.

Acknowledgments

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Literature Cited

Best, T. L. 1976. Morphologic variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Ph.D. Dissertation, Univ. Oklahoma, Norman. 90 pp.

———. 1978. Variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. J. Mammal., 59:160–175.

———. 1981. Bacular variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Southwest. Nat., 25:529–534.

———. 1982. Baja California kangaroo rat burrows and their relationships to ecogeographic and morphologic variation. J. Mammal., *In press*.

Gould, S. J., and R. F. Johnston. 1972. Geographic variation. Ann. Rev. Ecol. Syst., 3:457–498.

Hastings, J. R., and R. R. Humphrey. 1969. Climatological data and statistics for Baja California.

Univ. Arizona, Inst. Atmosph. Physics, Tech. Rept. Meteorol. Climatol. Arid Reg. No. 18. 96 pp.

Hastings, J. R., and R. M. Turner. 1965. Seasonal precipitation regimes in Baja California, Mexico. Geografiska Annaler, 47:204–223.

Kennedy, M. L., and G. D. Schnell. 1978. Geographic variation and sexual dimorphism in Ord's kangaroo rat, *Dipodomys ordii*. J. Mammal., 59:45–59.

Power, D. M. 1967. BIVAR, a FORTRAN IV program for general computer use. Version of June, 1967.

Rohlf, F. J., J. Kishpaugh, and S. Kirk. 1972. Numerical taxonomy system of multivariate statistical programs (NT-SYS). Version of October, 1972; State Univ. New York, Stony Brook.

Schnell, G. D., T. L. Best, and M. L. Kennedy. 1978. Interspecific morphologic variation in kangaroo rats (genus *Dipodomys*): Degree of concordance with genic variation. Syst. Zool., 27:34–48.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy/The principles and practice of numerical classification. W. H. Freeman and Co., San Francisco. 573 pp.

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