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CRANIAL VARIATION AMONG POPULATIONS OF THE
BLACK-TAILED PRAIRIE DOG IN NEW MEXICO

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Taxonomic relationships among populations have classically been derived from comparisions of skeletal morphology (Hall and Kelson, 1959; Sneath and Sokal, 1973). Populations of the same species that are similar in their morphometric traits and located close together geographically are usually considered to be genetically similar and, thus, comprise a uniform subspecies. Many studies have shown that geographically contiguous populations are similar in their skeletal dimensions (e.g., Kennedy and Schnell, 1978). However, studies examining species with patchy distributions have shown that phenetic relationships among populations may not exhibit geographic patterns, thereby making taxonomic classifications difficult (Berry *et al.*, 1978; Choate and Williams, 1978).

Populations of the black-tailed prairie dog, *Cynomys ludovicianus*, are widely separated from one another throughout their range from Canada to northern Mexico (Hall and Kelson, 1959). In the nineteenth century the distribution of prairie dogs was more or less continuous and their numbers were estimated at five billion (Seton, 1929). However, because of its alleged direct competition with livestock for forage and with agriculture for potential croplands, the prairie dog has been subject to attempted eradication by federal, state, and private interests (Koford, 1958; Smith, 1958; Cottam and Caroline, 1965; Madson, 1968). The distribution of prairie dogs has been reduced to relatively few scattered and somewhat isolated remnant populations. Reduction in potential

genetic exchange among populations of prairie dogs increases the probability of differentiation by genetic drift and founder effect (Mayr, 1963). Isolation by distance may have especially profound effects on the prairie dog due to its sedentary nature (King, 1955).

Hansen (1977) concluded that the morphology of prairie dogs from the Tularosa Basin in New Mexico was sufficiently different from that of prairie dogs from other regions to merit subspecific status (no subspecific name was proposed) for the animals from the Tularosa Basin. Because prairie dogs were rare in that region, he classified them as endangered, a status currently recognized by the New Mexico Department of Game and Fish. However, this author (Chesser, 1981) found that genetic heterogeneity among populations of prairie dogs in New Mexico was high even when compared over relatively short geographic distances. Genetic findings do not support previous taxonomic classifications of this species, and amount of differentiation among local populations is often greater than that among populations from widely spaced physiographic regions.

Classifications derived from analyses of morphology and electrophoretic data often do not correspond (Schnell *et al.*, 1978; Schnell and Selander, 1981). Therefore, the discrepancies between the results of previous studies (Hansen, 1977; Chesser, 1981) could be an artifact of the type of data used. Studies which concentrate on differences over large geographic distances may essentially ignore the possibility of heterogeneity over limited space. Such studies do not take into consideration isolation of prairie dog populations by man-caused and natural factors which may enhance heterogeneity over short distances. My purpose in this study was to examine the variation of cranial dimensions of black-tailed prairie dogs from populations separated by short and long geographic distances in New Mexico. Statistical methods were employed to investigate whether classical methods of classification are appropriate for species with disjunct patterns of distribution.

MATERIALS AND METHODS

A total of 17 skull measurements were recorded from 318 adult black-tailed prairie dogs (188 males, 130 females) collected from 18 localities in New Mexico (Fig. 1A; Table 1). Localities were designated (Chesser, 1981) according to four regions separated by major geological formations: (1) the Clayton region, north of the bluffs of the Llano Estacado; (2) the Roosevelt County region, on
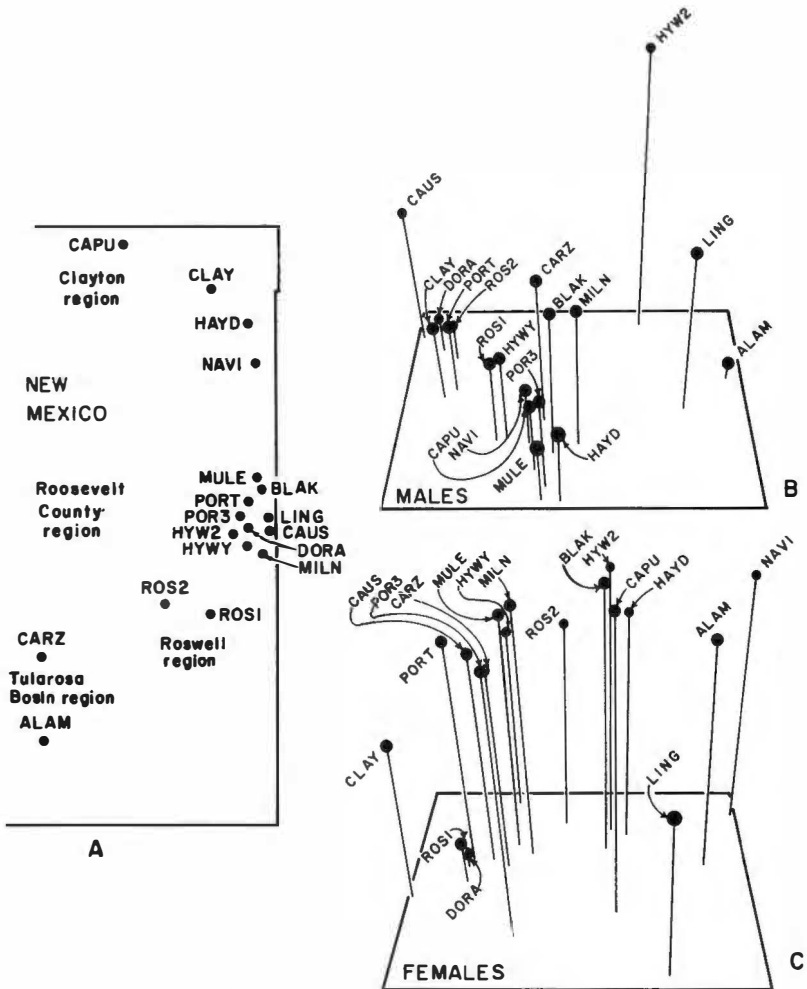
Fig. 1.—Map of collecting localities for black-tailed prairie dogs in New Mexico (A), and three-dimensional models depicting relationships among samples for male (B) and female (C) prairie dogs. The models were derived by principal components analysis using 17 cranial characters.

the Llano Estacado; (3) the Roswell region, on the premontane alluvial plain; and (4) the Tularosa Basin region, situated to the west of the Capitan Mountains. Prairie dogs from regions (1) and (2) are presently classified as *C. l. ludovicianus* (Hall and Kelson, 1959) whereas those from region (3) are *C. l. arizonensis* (Hall and Kelson, 1959) and those from region (4) represent the unnamed

TABLE 1.—*Collection localities of black-tailed prairie dogs in New Mexico. Sample abbreviations and regions refer to those depicted in Fig. 1A.*

Clayton Region

1. CAPU—8.5 km. NE Des Moines, Union Co., $n = 29$.
2. CLAY—12.8 km. S Clayton, Union Co., $n = 11$.
3. HAYD—9.6 km. E Hayden, Union Co., $n = 31$.
4. NAVI—10.7 km. SE Nara Visa, Quay Co., $n = 9$.

Roosevelt County Region

5. MULE—17.4 km. NE Portales, Roosevelt Co., $n = 7$.
6. BLAK—18.2 km. NE Portales, Roosevelt Co., $n = 14$.
7. PORT—9.5 km. E Portales, Roosevelt Co., $n = 78$.
8. POR3—19.1 km. S Portales, Roosevelt Co., $n = 9$.
9. CAUS—6.5 km. N Causey, Roosevelt Co., $n = 6$.
10. LING—2.0 km. SW Lingo, Roosevelt Co., $n = 5$.
11. DORA—3.5 km. W Dora, Roosevelt Co., $n = 11$.
12. HYW2—4.2 km. NW Hyway, Roosevelt Co., $n = 7$.
13. HYWY—1.0 km. E Hyway, Roosevelt Co., $n = 12$.
14. MILN—28.0 km. E Milnesand, Roosevelt Co., $n = 28$.

Roswell Region

15. ROS1—46.0 km. ENE Roswell, Chevas Co., $n = 7$.
16. ROS2—32.0 km. NNE Roswell, Chevas Co., $n = 9$.

Tularosa Basin Region

17. CARZ—31.0 km. W Carizozo, Lincoln Co., $n = 22$.
18. ALAM—17.5 km. NE Orogrande, Otero Co., $n = 21$.

endangered species (Hansen, 1977; previously designated *C. l. a.*, Hall and Kelson, 1959).

Cranial measurements (Fig. 2) were taken with dial calipers to the nearest 0.1 mm. as follows: (1) greatest skull length, (2) basal length, (3) rostral length, (4) nasal length, (5) upper diastemal length, (6) toothrow length, (7) premolar width, (8) third molar width, (9) rostral width, (10) palatine width, (11) post-palatal length, (12) length of auditory bulla, (13) width of auditory bulla, (14) greatest skull width, (15) mastoid breadth, (16) least interorbital width, and (17) greatest skull depth. Whenever possible, skull measurements were taken from the right side of the skull. Only adult prairie dogs with fully ossified skulls and completely closed cranial sutures were used in this study. This procedure reduced the variation in cranial dimensions attributable to animals of different ages since black-tailed prairie dogs appear to have determinant growth (King, 1955).

Univariate and multivariate statistics were used to analyze inter-locality differentiation and sexual dimorphism of cranial dimen-
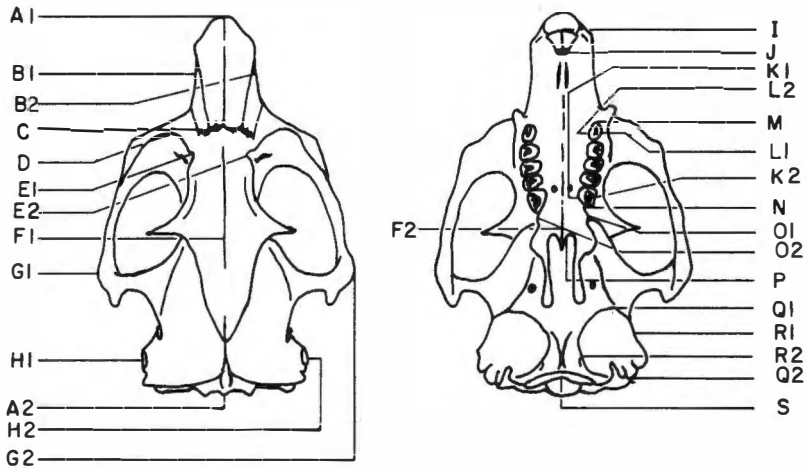
FIG. 2.—Skull measurements taken on adult black-tailed prairie dogs were as follows: greatest length (A1-A2); basalar length (I-S); rostral length (A1-D); nasal length (A1-C); diastemal length (J-M); maxillary toothrow length (M-N); palatine width (01-02); rostral width (B1-B2); third molar width (K1-K2); first premolar width (L1-L2); postpalatal length (P-S); auditory bulla length (Q1-Q2); auditory bulla width (R1-R2); greatest width of skull (G1-G2); mastoid breadth (H1-H2); least interorbital width (E1-E2); skull depth (F1-F2).

sions. Significant differences among locations for each character were analyzed by single classification analysis of variance tests and sums of squares simultaneous test procedure (SS-STP; Gabriel, 1964; Power, 1970). Multivariate analyses were performed using the subroutines from the NT-SYS (Rohlf *et al.*, 1974) and SAS (Barr *et al.*, 1976) computer programs. Matrices of Pearson's product-moment correlation coefficients between samples and characters were computed from standardized character values. Dendrograms of phenetic distance among samples and correlations among characters were prepared using the UPGMA (unweighted pair-group method using arithmetic averages) clustering method. The first three principal components and projections of samples were prepared from the matrix of phenetic distances and correlation among characters (Sneath and Sokal, 1973). Differences in cranial dimensions between the sexes were analyzed by single classification and multivariate analysis of variance. The proportion of character variability attributable to regional differences and intrapopulational variation was analyzed by variance components analysis (cf. Straney, 1976). Associations between matrices of phenetic distance and linear distance between locali-

ties were tested by Mantel's (1967; Sokal, 1979) general regression analysis (program from Chesser, 1980). The prairie dogs used in this study were also analyzed for electrophoretic variability in a previous study (Chesser, 1981). Classifications resulting from the phenetic and electrophoretic analyses were compared.

RESULTS AND DISCUSSION

The cranial dimensions for male black-tailed prairie dogs were significantly larger than those for females for 15 of the 17 characters measured (Table 2). In addition, the multivariate analysis of variance using all skull characters indicated a highly significant difference between the sexes ($P < 0.001$). Pizzimenti (1975) reported that prairie dogs were slightly to moderately sexually dimorphic and chose to combine measurements for the two sexes in subsequent analyses (Pizzimenti, 1976). Tileston and Lechleitner (1966) reported that external measurements of male and female black-tailed prairie dogs did not differ. Because of the significant differences between sexes in this study, all subsequent analyses were performed for each sex separately. This procedure reduced the sample sizes for each population. However, the matrices of phenetic distances among samples calculated for each sex were significantly associated (Mantel test, $t = 2.02$, $P < 0.05$; matrix correlation $= 0.28$), and no great distortion of sample relationships was apparent due to the data reduction.

Significant heterogeneity among localities is evident for 12 of the 17 characters for males and 15 of 17 for females (see Appendix I of Chesser, 1981, for character means for each sample). Length of the maxillary toothrow, width of the third molar, auditory bulla width, and upper diastemal length showed the greatest amount of interlocality variation for males. For females, variation among localities was high for width of the third molar, greatest skull length, greatest width of the skull, and basilar length. No significant variation among populations was found for rostral length, premolar width, post-palatal length, length of the auditory bulla, and interorbital width for males; and none was found for palatine width and premolar width for females (results of SS-STP tests are given in Appendix II of Chesser, 1981).

Character variation among the 18 samples was summarized by extraction of principal components. Three-dimensional projections are presented in Figures 1B and 1C for males and females, respectively. The loadings (correlations) of each character with each of the first three principal components are given in Table 2.

TABLE 2.—*Mean value (in mm.) for each of 17 characters measured for male (M) and female (F) prairie dogs, and results of analysis of variance (F-ratio) tests for sexual dimorphism. The loadings of each character on the first three principal components for each sex are also given.*

Character	Sex	Mean	F-ratio[1]	Principal components I	II	III
Skull length	M	6.25	65.63***	.961	−.111	.010
	F	6.07		.983	−.019	.085
Basal length	M	5.62	52.23***	.984	−.068	−.067
	F	5.44		.938	.235	.143
Rostral length	M	2.53	49.69***	.859	.053	.366
	F	2.26		.893	.130	−.053
Nasal length	M	2.37	49.98***	.717	.419	.375
	F	2.28		.838	−.404	.155
Diastemal length	M	1.54	12.65***	.702	.505	−.312
	F	1.51		.893	−.113	−.075
Toothrow length	M	1.62	7.23**	.117	−.834	.205
	F	1.60		−.185	.860	.168
Palatine width	M	0.88	1.85	.279	−.045	−.179
	F	0.87		.174	.164	−.836
Rostral width	M	1.13	1.36	.843	−.166	−.199
	F	1.12		−.035	−.035	−.902
Third molar width	M	0.39	5.02*	.621	.430	−.594
	F	0.38		−.063	−.204	.086
Premolar width	M	0.31	7.00**	.356	−.578	−.468
	F	0.30		.301	.229	−.344
Post-palatal length	M	2.23	29.64***	.834	.089	.194
	F	2.15		.890	−.345	−.011
Auditory bulla length	M	1.14	17.75***	.469	.449	−.187
	F	1.11		.488	.288	−.462
Auditory bulla width	M	1.04	12.66***	.823	−.132	.052
	F	1.01		.593	−.328	.172
Skull width	M	4.44	45.01***	.769	−.278	−.216
	F	4.29		.921	−.108	.102
Mastoid breadth	M	2.72	38.38***	.805	−.390	−.134
	F	2.64		.593	.682	.244
Interorbital width	M	1.33	20.37***	.490	.519	.494
	F	1.28		.401	.810	.072
Skull depth	M	1.92	71.66***	.634	−.380	.533
	F	1.86		.436	−.229	−.259

[1]Degrees of freedom for each test are 1,317.
*P < 0.05; **P < 0.01; ***P < 0.001.

The values for the character loadings for males and females were generally similar. The amount of phenetic variation represented by the first three principal components for males and females, respectively, was: 49.6 and 42.6 for component I, 15.1 and 15.3 for component II, and 10.2 and 12.4 for component III. The total

variability explained by the first three principal components was 74.9 for males and 70.3 for females.

Characters with high loadings on principal component I were ones that reflected the overall size of the skull. Measurements such as palatine width, premolar width, and auditory bulla width, as well as measurements of skull depth and least interorbital width, had low associations on the first component. Rostral width and third molar width had relatively high loadings for males but not for females. Samples which had large overall skull dimensions are depicted towards the right-hand side of Figs. 1B and 1C.

Component II had high loadings for maxillary toothrow length and greatest skull length for both males and females, mastoid breadth for females only, and premolar width and upper diastemal length for males. Maxillary toothrow length for females and premolar width for males had negative loadings. All of the other high loadings had positive values. Thus, females with relatively short toothrows, deep skulls, and wide mastoidal breadth are depicted towards the front of Fig. 1C; samples for males depicted near the front of Fig. 1B had narrow premolars, long toothrows, and large diastemal lengths.

Component III had high loadings for palatine width and rostral width and a moderately high value for length of the auditory bulla in females. Males had relatively high loadings for the third molar width, premolar width, skull depth, and least interorbital width. Samples for females from populations with low values for auditory bulla length, palatine width, and rostral width are depicted high above the base of Fig. 1C. In contrast, males with small premolar widths, deep skulls, and broad interorbital widths are illustrated by the points high on the figure.

Samples within the four regions did not fall into distinct clusters. The two populations within the Tularosa Basin, CARZ and ALAM, which together have been proposed as an endangered subspecies (Hansen, 1977), are widely separated (Figs. 1B, 1C). Prairie dogs from the ALAM population did have consistently larger cranial dimensions than animals from most other populations, but this large size was not shared by CARZ animals or those from the nearby Roswell region (ROS1 and ROS2; *C. l. arizonensis*). Neither morphological nor genic data (Chesser, 1981) for prairie dogs support the designation of all Tularosa Basin populations as a single endangered subspecies, and thus Hansen's (1977) classificatory recommendations are not supported by my findings.

In addition, *C. l. arizonensis* does not appear to possess any unique characteristics to substantiate a separate subspecies in this

region of New Mexico. The strong variation among local populations poses some unique logistical problems for the systematic classification of organisms. The reason the Tularosa Basin prairie dogs and those of the Roswell region did not meet the criteria of a separate subspecies was not because they were found to be similar to other groups, but rather because all of the populations were apparently different and no distinct classification could be made. Thus, two options are available regarding the taxonomy of populations of prairie dogs: the first would be to designate a large number of subspecies of prairie dogs; the second and more tenable option is to lump them together as a single subspecies. Thus, the conclusions of this study are: (1) prairie dogs from the Tularosa Basin region do not constitute a separate subspecies, and (2) there is no basis for considering that the populations in the Roswell and Tularosa Basin regions represent a separate subspecies other than *C. l. l.* Conclusions regarding the status of the *C. l. a.* complex to the west and south of the Tularosa Basin cannot be made without further studies.

Differences of cranial morphology between populations separated by short distances were particularly evident for samples within Roosevelt County. Samples from populations separated by as little as 15 km. did not cluster together (e.g., CAUS-LING, HYWY-HYW2; Figs. 1B and 1C). Apparently, as was concluded in the genetic study (Chesser, 1981), differences between local populations are at times as great as those between populations in different regions. Factors such as the sedentary nature of prairie dogs (King, 1955), the disruption of continuous suitable habitat by ranching and agriculture (Koford, 1958), and the decimation of populations by poisoning practices (Collier and Spillett, 1975) may reduce successful dispersal among populations and enhance random differentiation. The low similarity in cranial morphology between neighboring populations was emphasized by the lack of association between matrices of phenetic and the reciprocal of linear geographic distances.

The results of the variance component analysis (Table 3) elucidate the relative importance of interlocality versus interregional sources of variability for cranial dimensions. The majority of the variability was not accounted for by samples compared within regions or samples compared between regions. Although the amount of variability accounted for by comparing samples within and between regions was at times considerably different for the two sexes, the overall means were similar. The amount of variation attributable to differences among locations was almost three times

TABLE 3.—*Percentage of morphological variability accounted for by differences among samples within regions (locations), among regions, and within locations for each of 17 skull characters measured for male and female black-tailed prairie dogs.*

Skull character	Males			Females		
	Within regions	Among regions	Within locations	Within regions	Among regions	Within locations
Skull length	15.4	3.1	81.5	23.0	4.3	73.7
Basal length	9.7	6.1	84.2	17.2	1.7	81.1
Rostral length	9.0	0.3	90.7	6.7	1.6	91.7
Nasal length	19.8	1.7	78.5	11.6	1.5	86.9
Diastemal length	1.8	15.9	82.3	13.3	2.2	84.5
Toothrow length	33.0	2.2	64.8	7.8	0.2	92.0
Palatine width	0.0	6.9	93.1	0.0	3.5	96.5
Rostral width	7.6	2.9	89.5	1.1	0.3	98.6
Third molar width	1.7	19.7	78.6	20.9	2.0	77.1
Premolar width	14.5	0.2	85.3	2.6	0.3	97.1
Post-palatal length	8.7	1.6	89.7	9.4	4.2	86.4
Auditory bulla length	0.0	3.7	96.3	0.0	9.0	91.0
Auditory bulla width	25.0	0.2	74.8	17.8	3.5	78.7
Skull width	12.6	1.3	86.1	15.0	7.7	77.3
Mastoid breadth	8.3	2.5	89.2	9.6	2.2	88.2
Interorbital width	2.1	0.4	97.5	8.3	3.3	88.4
Skull depth	8.2	4.2	87.6	10.4	2.2	87.4
Mean	10.4	4.3	85.3	10.3	2.9	86.8

greater than that among the four regions for all cranial characters except upper diastemal length and width of the third molar for males, and palatine width and auditory bulla length for both males and females.

The average amount of morphometric variability explained by location within regions and among regions was almost identical to the amount of gene diversity (Nei, 1975) explained by these same two sources of variation (Chesser, 1981, location = 10.31%; region = 3.56%). Even though the patterns of variability for morphometric and electrophoretic data were similar, the matrices of phenetic and genetic distances between populations were not significantly associated ($P > 0.30$ for both males and females; $P > 0.20$ when data for males and females were combined). Thus, as in the case for kangaroo rats (Schnell *et al.*, 1978), classifications based on skeletal and electrophoretic data are not consistent. If stochastic factors were the primary causes for producing the differences among populations with little or no dispersal between them, the distributions of phenetic and genetic variabilities may be expected to be similar. Stochastic and/or selective forces probably affect phenetic and electrophoretic characters differently (e.g.,

Wright, 1980). Thus, systematic relationships between populations based on the two types of data may not be associated, whereas the overall amounts of variation among samples may be comparable.

The conclusions of this study are similar to those from the author's (Chesser, 1981) genetic analysis of prairie dogs. There is considerable variation among samples in close proximity, and the intraregional variability is far more pronounced than that found between regions. No geographic or subspecific relationships are evident. Erratic geographic variation among samples is not unusual, especially when populations are somewhat isolated and the possibility of reciprocal genetic exchange is or has been limited (Berry et al., 1978; Choate and Williams, 1978). The distribution of prairie dogs was somewhat continuous 75 to 100 years ago before poisoning and agricultural practices reduced their range (Seton, 1929). It is doubtful, however, that all phenetic and genetic differentiation has taken place since that time. Prairie dogs have probably always had disjunct patterns of variation due to their complex social organization and low dispersal rates (King, 1955), and the high degree of variation among nearby samples hinders the identification of variables that would characterize distinct subspecific groups.

The above arguments do not rule out the possibility of significant geographic trends. If samples were analyzed over the entire range of black-tailed prairie dogs, significant regional trends would probably be evident (cf. Pizzimenti, 1975); however, the variation within any specific region would most likely be similar to that described in this paper. The classical definition of a subspecies (e.g., "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the speecies and differing taxonomically from other populations of the species"; Mayr, 1963, p. 210) is probably not applicable to prairie dogs. Progressive reduction of the distribution of prairie dogs to scattered, isolated populations within all portions of its range will continue to enhance local differentiation of populations.

Literature Cited

Barr, J. A., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A user's guide to SAS. SAS Institute Inc., Raleigh, North Carolina.

Berry, R. J., M. E. Jakobson, and J. Peters. 1978. The house mice of the Faroe Islands: a study in microdifferentiation. J. Zool., London, 185:73-92.

Chesser, R. K. 1980. Computer systems and programming for the analysis of population genetics data. Spec. Publ. Univ. Stockholm, 3:1-60.

———. 1981. Genetic and morphologic variation within and among populations of the black-tailed prairie dog. Unpublished Ph.D. dissertation, Univ. Oklahoma (Norman), 90 pp.

Choate, J. R., and S. L. Williams. 1978. Biogeographic interpretation of variation within and among populations of the prairie vole, *Microtus ochrogaster*. Occas. Papers Mus., Texas Tech Univ., 49:1-25.

Collier, G. D., and J. J. Spillett. 1975. Factors influencing the distributions of the Utah prairie dog, *Cynomys parvidens* (Sciuridae). Southwestern Nat., 20:151-158.

Cottam, C., and M. Caroline. 1966. The black-tailed prairie dog in Texas. Texas J. Sci., 17:294-302.

Gabriel, K. R. 1964. A procedure for testing homogeneity of all sets of means of analysis of variance. Biometrics, 20:459-477.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press Co., New York, 1:xxx+1-546+79, 2:viii+547-1078+79.

Hansen, D. 1977. Taxonomic status of the prairie dog subspecies *Cynomys ludovicianus ludovicianus* (Ord) and *Cynomys ludovicianus arizonensis* Mearns. Unpublished master's thesis, Eastern New Mexico Univ., 71 pp.

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

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol., Univ. Michigan, 67:1-123.

Koford, C. B 1958. Prairie dogs, white-faces and blue gramma. Wildl. Monogr. 3:1-78.

Madson, J. 1968. Dark days in dogtown. Audubon, 70:32-43.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res., 27:209-220.

Mayr, E. 1970. Populations, species, and evolution. Belknap Press of Harvard Univ. Press, Cambridge, xv+1-453 pp.

NEI, M. 1975. Molecular population genetics and evolution. North-Holland Research Monographs. North-Holland Publishing Co., Amsterdam, 40: xii+288 pp.

PIZZIMENTI, J. J. 1975. Evolution of the prairie dog genus *Cynomys*. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 1-73.

———. 1976. Genetic divergence and morphological convergence in prairie dogs, *Cynomys gunnisoni* and *Cynomys leucurus*. I. Morphological and ecological analyses. Evolution, 30:345-366.

POWER, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. Univ. Kansas Publ., Mus. Nat. Hist., 19:1-83.

ROHLF, F. J., J. KISHPAUGH, R. BARTCHER, AND K. KIRK. 1974. NT-SYS. Numerical taxonomy system of multivariate statistical programs. State Univ. New York, Stony Brook, 87 pp.

SCHNELL, G. D., T. L. BEST, AND M. L. KENNEDY. 1978. Interspecific morphologic variation in kangaroo rats (*Dipodomys*): degree of concordance with genic variation. Syst. Zool, 27:34-48.

SCHNELL, G. D., AND R. K. SELANDER. 1981. Environmental and morphological correlates of genetic variation in mammals. Pp. 60-99, *in* Mammalian population genetics (M. H. Smith and J. J. Joule, eds.). Univ. Georgia Press, Athens, xi+380 pp.

SETON, E. T. 1928. Lives of game animals. Doubleday, Doran and Co., Garden City, New York, 4:xxii+1-949 pp.

SMITH, R. E. 1958. Natural history of the prairie dog in Kansas. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 16:1-36.

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, xv+573 pp.

SOKAL, R. R. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool., 28:227-232.

STRANEY, D. O. 1976. Variance partitioning and nongeographic variation. J. Mamm., 59:1-11.

TILESTON, J. V., AND R. R. LECHLEITNER. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. Amer. Midl. Nat., 75:292-316.

WRIGHT, S. 1980. Genic and organismic selection. Evolution, 5:825-842.

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