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GENETIC AND MORPHOLOGIC VARIATION WITHIN AND AMONG POPULATIONS OF THE BLACK-TAILED PRAIRIE DOG

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THE UNIVERSITY OF OKLAHOMA

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GENETIC AND MORPHOLOGIC VARIATION WITHIN AND AMONG POPULATIONS OF THE BLACK-TAILED PRAIRIE DOG

A DISSERTATION

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BY

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GENETIC AND MORPHOLOGIC VARIATION WITHIN

AND AMONG POPULATIONS OF THE BLACK-TAILED

PRAIRIE DOG

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PREFACE

The black-tailed prairie dog once inhabited a large and rather continuous range of grassland prairie throughout the central and western United States. However, agricultural and poisoning practices have reduced their distribution to relatively few, scattered remnant populations. There is a paucity of information on the systematic relationships among prairie dogs from different areas and virtually no knowledge of the genetic variability contained in this species. Therefore, in 1977 I began an assessment of the amounts and distributions of morphometric and genetic variation of the black-tailed prairie dog in New Mexico. The goal of the study was to document the systematic status of prairie dogs from different regions of the state and to determine the pattern of genetic differentiation both among and within populations.

The study was written in two sections: (1) genetic variability within and among populations of the black-tailed prairie dog; and (2) cranial variation among populations of the black-tailed prairie dog. Each section was written in the form of a paper for a specific scientific journal. The first paper (genetic variability) will be submitted to Evolution and the second (cranial variation) will be sent to the Journal of Mammalogy. Additional material not to be included in the publications but important for reference information has been included in Appendices I and II.

GENETIC VARIABILITY WITHIN AND AMONG POPULATIONS OF THE BLACK-TAILED PRAIRIE DOG

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Genetic heterogeneity over short geographic distances may now be viewed as the rule rather than the exception (Smith et al. 1978; Wright 1978) even for large, highly mobile species such as the elephant (Osterhoff et al. 1974), moose (Ryman et al. 1977, 1980), red deer (Gyllensten et al. 1980), and white-tailed deer (Chesser et al. in press; Manlove et al. 1976). For most studies of the genetic structure of populations the specific mechanisms of genetic differentiation have not been identified. To understand the causes of population subdivision more fully, comparison of genetic variability should be made among the breeding units, rather than arbitrarily selected samples. Allele frequency differences among observed social groups within populations have been documented for house mice (Selander 1970), dark-eyed juncos (Baker and Fox 1978), marmots (Schwartz and Armitage 1980), and man (Neel and Ward 1972). The organization of populations into somewhat independent breeding units may have important effects on the short-term evolution of populations (Wright 1980) as well as on the maintenance of genetic polymorphisms (Chesser et al. 1980; Karlin and Campbell 1980).

The black-tailed prairie dog (Cynomys ludovicianus) is perhaps the most socially complex of any rodent species (King 1955; Koford 1958) and may present a spatially complex population structure. Prairie dog populations are comprised of several small coteries (harems) which are defended by a single dominant male associated with a harem of two to eight mature females (King 1955). Activity and mating of the prairie dogs are usually confined to the coterie areas. The coteries are in turn organized into larger population units (wards) which are separated by areas of unsuitable habitat (e.g., trees, hills, sand; King 1955). Dispersal of prairie dogs between coteries within wards is greater than that among wards, and dispersing animals are predominantly males (King 1955). Thus, it appears that genetic heterogeneity may occur both among coteries within wards and among wards within populations of black-tailed prairie dogs due to low rates of successful dispersal.

Not only may genetic differentiation occur among breeding units within populations, but it may be particularly high among populations. Agricultural, ranching and poisoning practices have reduced the local distributions of prairie dogs in most areas to relatively few, scattered populations (Koford 1958). Barriers to dispersal imposed by unsuitable habitat and/or distance as well as dramatic reductions in population sizes may have resulted in differentiation among populations over short as well as long geographic distances. On the basis of cranial morphology, Hansen (1977) concluded that the prairie dogs from the Tularosa Basin in New Mexico were sufficiently different from those of other regions to merit their classification as an endangered subspecies. Hansen's (1977) results suggest that gene flow among prairie dogs from separated regions must be somewhat lower than that among populations within the regions.

The complex organization of breeding units within populations of prairie dogs and the disjunct pattern of distribution of populations over wide geographic areas provide an opportunity to investigate the relative importance of social and ecological factors on the organization of genetic variability. The purpose of this study was to examine the association of the social organization and genetic differentiation within populations of the black-tailed prairie dog.

Genetic differences among populations both in close proximity and those separated by long geographic distances were investigated, and the magnitude of genetic variability accounted for by the various levels of organization was analyzed.

MATERIALS AND METHODS

Black-tailed prairie dogs (n = 509) were collected from 21 locations in New Mexico (Fig. 1). Liver samples were taken and labeled according to each animal's sex and location and then frozen in liquid nitrogen. The liver samples were homogenized in a buffered saline solution in the laboratory and stored at -70 C until electrophoresis was performed.

The homogenate was analyzed using standard starch-gel electrophoretic techniques (Selander et al. 1971). Of 16 loci analyzed, seven were polymorphic (frequency of the common allele in at least one population < 0.99; unless otherwise noted, staining procedures follow those of Selander et al. 1971): adenosine deaminase (ADA; Harris and Hopkinson 1977), glutamate dehydrogenase (GDH), glutamic oxalacetic transaminase-2 (GOT-2), mannosephosphate isomerase (MPI; Nichols et al. 1973), nucleoside phosphorylase (NP; Harris and Hopkinson 1977), 6-phosphogluconate dehydrogenase (6-PGD), and phosphoglucomutase-2 (PGM-2). No variability was found for the nine loci: glucose phosphate isomerase, GOT-1, isocitrate dehydrogenase, lactate dehydrogenase-1 and -2, mannose dehydrogenase, malic enzyme, PGM-3, and sorbitol dehydrogenase. Additional loci were analyzed, but the banding patterns were not consistantly scorable. Data for only the polymorphic loci were used in the statistical analyses. The generally most common allele for each variable locus was designated as the "100" allele and additional alleles were numerically designated according to the mobility of their products relative to that of the common allele.

Prairie dogs from the 21 populations (Fig. 1) were identified as belonging to one of the following regions: (1) Tularosa Basin region (CARZ and ALAM populations) with prairie dogs from this area classified as an endangered subspecies by Hansen (1977); (2) Roswell region (ROS1 and ROS2 populations) with prairie dogs from this region classified as _C. l. arizonensis_ (Hall and Kelson 1959); (3) Clayton region (CAPU, CLAY, HAYD, NAVI and SAJO populations) with prairie dogs from populations north of the Llano Estacado; and (4) Roosevelt County region (12 populations). Ward boundaries were determined for four of the populations (CAPU, CLAY, PORT and POR3). A series of transect lines 20 m apart were surveyed in both north-south and east-west directions in three of the four wards of the PORT population. Wooden stakes were placed in the corners of each 400-m^2 quadrat. Movements of prairie dogs within and between the quadrats were observed and noted from an elevated blind. Distinct, nonoverlapping areas of activity and zones of antagonistic behavior among neighbors were observed for several groups of prairie dogs within the wards. These groups were assumed to represent coteries. Prairie dogs collected from populations CAPU, CLAY, PORT and POR3 were identified as to their appropriate ward, and coteries were noted for animals from the PORT population.

The genetic differentiation of prairie dogs among and within the populations was analyzed by using Wright's (1965) _F_-statistics as modified by Nei (1977). The bias in genotypic proportions due to small sample sizes was corrected for using Levene's (1949) correction, and the resulting values were incorporated into the calculation of the *F*-statistics. Significance of gene frequency differences among populations was tested for each locus by the chi-square test,

$$X^2 = 2NF_{ST}(k-1)$$

with (k-1)(s-1) degrees of freedom, where N is the total sample size, k is the number of alleles for the locus, and s is the number of populations (Workman and Niswander 1970). The F_{ST} value was corrected for the binomial sampling variance as $F_{ST}=F_{ST}-(1/2N)$, (Workman and Niswander 1970). All *F*-values were calculated using weighted (by sample sizes) means and variances of allele frequencies. Thus, the chi-square tests described above gave identical results as k X s contingency tests of observed allele counts.

Genetic identities (Nei 1972) between each pair of populations were calculated, and the relationships among populations were summarized in the form of a dendrogram derived from the UPGMA (unweighted pair group method using arithmetic averages; Sneath and Sokal 1973) clustering method. The relationship among matrices of genetic identity and linear, geographic distances (in kilometers) between populations were tested using the general regression method developed by Mantel (1967; also see Sokal 1979). Statistical analyses were performed using the computer programs of Rohlf et al. (1974) and Chesser (1980). Significance was indicated when the probability of obtaining the observed results was less than 5 per 100 trails (α<0.05).

RESULTS

The allele frequencies for the seven variable loci for animals from each population and ward are given in Table 1. Variability for the MPI locus was not found for prairie dogs outside of the Clayton region and a unique allele for 6-Pgd (122) was observed only within the POR3 population. The genetic identities between pairs of populations are summarized in Fig. 2. Mantel (1967) regression tests indicated that the matrices of genetic identities and linear distances between populations were not significantly associated with one another (t_∞=1.24; $\underline{P}$>0.20; matrix correlation [$\underline{r}$]=0.11), nor were matrices of genetic identities and the reciprocals of linear distances (t_∞=1.37; $\underline{P}$>0.10; $\underline{r}$=0.15).

Results of the analysis of the standardized variance of allele frequencies ($\underline{F_{ST}}$'s) indicated significant differentiation for prairie dogs among all populations as well as among those from populations within each of the four regions (Table 2). The differentiation of allele frequencies was significant for all variable loci when data from all populations were combined. Heterogeneity of allele frequencies was not significant for ADA and MPI for prairie dogs within any of the regions, 6-PGD for those from the Tularosa basin and Roswell regions, and NP for animals within the Roswell region. The high positive values for $\underline{F_{IT}}$ indicated a greater number of homozygous individuals relative to that expected when data were pooled for all populations. This result was not surprising given the high $\underline{F_{ST}}$ values (Wahlund 1928). The high positive $\underline{F_{IS}}$ values indicated that, on the average, there was an excess of homozygous animals within each population. Therefore, relatively high levels of inbreeding and/or further subdivision within the populations is likely.

Significant heterogeneity of allele frequencies within populations was found for prairie dogs from the different wards within the CAPU, PORT, and POR3 populations, but not for those from the CLAY population (Table 3). Again, the high $\underline{F}_{IT}$ values were expected, but the high positive $\underline{F}_{IS}$ values (except for that of POR3) indicated high levels of inbreeding within the wards. The analysis of $\underline{F}_{ST}$ values calculated from allele frequencies for prairie dogs from coteries where at least three animals were collected (Fig. 3) in the PORT population showed significant genetic differentiation for prairie dogs within each of the three wards and when data were combined (Table 3).

The results of an analysis of gene diversity (Nei 1973, 1975) of prairie dogs from the various hierarchical combinations of wards (W), populations (S), and regions (R) within the total (T) of all populations are given in Table 5. On the average, approximately 10% of the total variance of allele frequencies was due to the genetic differences of prairie dogs from the populations ($\underline{G}_{PT}$=.1031); that is, 90% of the total gene diversity is found in prairie dogs within any given population (1-$\underline{G}_{PT}$). About 88 and 96% of the total gene diversity was accounted for by prairie dogs within wards and regions, respectively (1-$\underline{G}_{WT}$ and 1-$\underline{G}_{RT}$), whereas, 93% of the total genetic variation exists within any population in a region (1-$\underline{G}_{PR}$).

The genetic differences of prairie dogs among the regions were greater than those within the regions for only two loci, MPI and 6-PGD. The differentiation among regions from these two loci is attributable to "unique" variation within the Clayton region.

Variation for MPI was only observed within the Clayton region and variability for the 6-PGD locus was considerably lower in the Clayton than in other regions. Average heterozygosity for 6-PGD was 0.114 for prairie dogs in the Clayton region, whereas, values of 0.443, 0.310, and 0.340 were observed within the Roosevelt County, Roswell, and Tularosa basin regions, respectively. The Got-2-100 allele was fixed within the Roswell and Tularosa Basin regions. However, this locus was sporadically fixed in various populations within other regions (Table 1) and heterogeneity among regions only accounted for 3% of the total variation for this locus (Table 4).

DISCUSSION

Geographic variation.--The results of the present study indicate that considerable genetic divergence has occurred among populations of the black-tailed prairie dog. The average differentiation among populations is about 10% (F_{ST}=.1031; Table 2) which is similar to the values obtained for moose from different Scandinavian countries (9%; Ryman et al. 1980) and house mice from different farms (12%; Nei 1975, p. 152). The estimated amount of absolute gene differentiation among the populations (D_m=0.15) is equal to that observed among the major races of man and among populations of house mice (Nei 1975, p. 152).

The patterns of genetic similarity among populations do not show any clear trends either between or among the regions studied (Fig. 2). The pronounced spatial heterogeneity and lack of association of genetic and linear distances are in agreement with the expectations of a model of differentiation by founder effect (Mayr 1963), mutation, and genetic drift (Fuerst et al. 1977; Chakraborty et al. 1978). An extreme example of the probable results of founder effect and genetic drift is provided by the analysis of genetic variability for prairie dogs from population NAVI. The great divergence of this population (Fig. 2) is primarily due to the near fixation of the otherwise rare Np-55 allele (Table 1). The high frequency of the Pgm-2-89 allele within the NAVI population also contributed to the low genetic identity of the NAVI with other populations. The 6-Pgd-122 allele was only observed for prairie dogs from the POR3 population (Table 1), although other nearby (< 10 km) populations were sampled. The dramatic differences of allele frequencies and the presence of unique alleles for prairie dogs from proximal populations indicates that dispersal among local populations must be infrequent.

The relative amount of genetic differentiation among populations within the regions was about two-thirds ($\underline{G}_{\underline{PR}}/\underline{G}_{\underline{PT}}$), whereas, the value for prairie dogs among the regions was one-third ($\underline{G}_{\underline{RT}}/\underline{G}_{\underline{PT}}$). These results are similar to those for localities within countries, and among countries, respectively, for the Scandinavian moose (Ryman et al. 1980). The genetic differences of prairie dogs among the regions are greater than those within a region for only two loci, MPI and 6-PGD. The differentiation among regions for these two loci is attributable to unique variation within the Clayton region. Variation for MPI was only observed for prairie dogs within the Clayton region and variability for the 6-PGD locus was considerably lower in the Clayton than in other regions (Table 1). The result that genetic differentiation was greater among populations within regions than that among regions was somewhat surprising since the regions were separated by major geographical barriers such as mountains and rivers.

The patterns of genetic identities and differentiation of prairie dogs from the various populations and regions are not supportative of the subspecies classifications reported by Hall and Kelson (1959; *C. l. arizonensis* = Roswell and Tularosa Basin regions, *C. l. ludovidianus* = other regions) nor do they suggest that the prairie dogs from the Tularosa Basin are substantially genetically different from those from other parts of their range (Hansen 1977). However, conclusions based on electrophoretic and morphometric data often do not correspond (Schnell et al. 1978; Schnell and Selander 1981) and decisions regarding the systematic status of this species should await further investigation (see Chesser 1981).

Variation within populations.--In addition to the obvious barriers to dispersal among populations (e.g., distance, mountains, rivers) colonial species also face the obstacles to short-distance movements imposed by intraspecific antagonistic behavior (e.g., territoriality). The average genetic differentiation among wards within a population was about 5% (F_{ST}=G_{WP}=0.045 to 0.065; Table 3). The G_{WP} value of 0.022 (Table 4) is an underestimate because most populations were assumed to be comprised of a single ward. Thus, heterogeneity among wards is slightly greater than that among house mice from different barns or farms (F_{ST}=0.025 and 0.047; Selander and Kaufman 1975), among deer from different hunting areas (F_{ST}=0.035; Smith et al. in prep.) and for Indians from different villages (F_{ST}=0.040; Nei 1975), but is slightly lower than that for marmots from different colonies (F_{ST}=0.07; Schwartz and Armitage 1980). The geographic distance among population units in the forementioned studies were usually much greater than that between the wards of a prairie dog population and restriction of movements among wards is almost certainly due to behavioral rather than geographic inhibition.

The results of the analysis of genetic heterogeneity among prairie dogs from different coteries within the wards of the PORT population showed that the social organization has dramatic effects on the distribution of genotypes within a population. On the average, genetic differences among the coterie populations are 23% of those of complete differentiation (Table 3), and the positive values for F_{IS} indicate relatively high degrees of inbreeding within the coteries. Although the F_{ST} values are slightly inflated by sampling errors since I obtained only a few animals from many of the coteries, the largest possible values of this bias is 0.040 ($\bar{p}\bar{q}/2N$; Nei and Imaizumi 1966), which is small when compared to the mean of 0.227. This is one of the highest F_{ST} values reported for natural populations, especially over such short distances. However, most previous genetic comparisons have been made among arbitrarily selected population subdivisions which do not conform to the actual breeding units. Lumping the breeding units of a population would usually serve to decrease the F_{ST} values while increasing the F_{IS} and F_{IT}. If the breeding units of other natural populations could be identified and compared, similar degrees of genetic differentiation to those reported here would probably not be unusual.

Inbreeding and genetic drift are expected within coteries due to their small size and skewed sex ratio. Coteries are usually comprised of a single breeding male and two to eight breeding females (King 1955). The expected effective population size (N_e) within each coterie, therefore, is approximately 3.5 (Crow and Kimura 1970). Since the inbreeding coefficient increases each generation at a rate which is proportional to the effective population size, $1/2N_e$, (Falconer 1960), the observed differentiation among coteries could be accomplished in two generations of breeding. Males may occasionally mate with their daughters or mothers as females seldom leave their native coterie (King 1955).

If disperal among population units is sufficient only to counterbalance the effects of genetic drift (i.e., constant F_{ST}), the heterogeneity among animals from the units can be estimated as $F_{ST}=1/(4N_e m+1)$, where m is the dispersal rate (Wright 1969). The number of dispersers among population units necessary to maintain a given level of differentiation for neutral alleles can be estimated by $N_e m=(1/4F_{ST})-.25$ (e.g., Ryman et al. 1980; Stahl 1980). The number of dispersing prairie dogs necessary to maintain the observed differentiation among coteries within a ward is about one per generation (estimates for my samples range from 0.90-1.39) and less than one per generation (0.85) among all coteries. The number of dispersers necessary to maintain the genetic differences among prairie dogs from different wards is about five (3.58-5.35) per generation. The apparent low dispersal rate within populations of prairie dogs may be indicative of the difficulties for animals to enter nonparental social groups (King 1955).

Both behavioral and physiographic restrictions to reciprocal genetic exchange among the various population units have important effects on the apportionment of overall gene diversity. About 88% ($1-G_{WT}$; Table 5) of the total gene diversity of prairie dogs in New

Mexico exists within the wards of a population. Only 72% of the total gene diversity is found within the coteries of the PORT populations. These results are in general agreement with Lewontin's (1972) conclusion that a large portion of the genetic variation exists within the small units of populations. The total gene diversity found within the actual breeding units of the populations in this study is lower than that found by Lewontin (72 vs 88%). The average prairie dog contains about 95% of the gene diversity within his native coterie and approximately 68% (.95 x .72) of the total gene diversity for prairie dogs in New Mexico.

What are the advantages of the colonial behavior of prairie dogs? Hoogland (1977, 1979b) concluded that protection from predators is the single benefit of prairie dog coloniality while several disadvantages such as increased aggression, increased transmission of diseases and parasites, misdirection of parental care, and increased conspicuousness to predators were found (Hoogland 1979a). Another obvious disadvantage for individuals in small inbreeding populations is inbreeding depression of fitness (Falconer 1960). However, breeding among related individuals increases the proportion of their genome which is passed on to their offspring. When the potential costs of dispersal are high it may be advantageous for an individual to mate with its relatives (Bengtsson 1978). The difficulties associated with entering social groups and increased exposure to predation certainly increases the potential costs for prairie dog dispersal. It is probable that the advantages of certain levels of inbreeding outweigh the costs detailed by Hoogland (1979).

An immediate consequence of inbreeding and drift is that certain allelic combinations are exposed to selection in more homozygous states (Wright 1980). Selectively advantageous gene combinations increase in frequency more quickly in small inbreeding demes than in larger panmictic populations (Slatkin 1976). Thus, small semi-isolated demes within populations may serve as reservoirs of unique gene combinations, with a concomitant result that overall genetic variability will be maintained in structured populations for long periods of time (Christiansen 1974, 1975; Chesser et al. 1980; Karlin and Campbell 1980). Predominant disperal by only one sex, as is the case in prairie dogs, may increase the probability of maintaining polymorphisms since one sex (e.g., females) always has territories in which to breed and propagate its genome. Thus, the selective advantages of inbreeding for individuals may result in heterogeneous populations with long-term maintenance of genetic polymorphisms (e.g., Altukov 1974).

Genetic differences over short distances for animal populations may be the rule rather than the exception (Smith et al. 1978). However, the genetic subdivision reported here is on a much finer scale than that yet reported for any vertebrate with the exception of that for house mice within barns (Selander 1970). The social behavior of prairie dogs is among the most complex observed among vertebrates (King 1955). The result of the social structuring is a mosaic of gene combinations over short distances and rapid inbreeding and genetic drift within the social groups. On a larger scale, genetic differences among populations are accrued by low dispersal rates between populations. Increased agricultural use of land and associated ranching practices as well as wide-spread poisoning programs, have undoubtedly reduced dispersal among prairie dog populations. As a result, the genetic differences among prairie dogs from local populations are often as great as those from vastly different parts of their range.

SUMMARY

Genetic variation for seven variable loci was analyzed for prairie dogs within and between populations in eastern New Mexico. Significant genetic differentiation was found for prairie dogs from populations in close proximity (5-15 km) as well as for those from distant parts of their range. The degree of local differentiation was greater than that among regions separated by major geographical barriers. The patterns of genetic similarities between prairie dogs from different populations were not in agreement with proposed taxonomic classifications. Significant heterogeneity of allele frequencies was found for prairie dogs from different wards (portions of a population separated by unsuitable habitat) within a population, as well as for those from different coteries (harem groups) within the wards. The social behavior of prairie dogs has resulted in genetic differentiation over very small distances and rapid inbreeding and genetic drift within the social groups. The mechanisms and consequences for sustaining such fine scale subdivision are discussed.

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Table 1. Allele frequencies of seven variable loci for black-tailed prairie dogs from various regions and populations in New Mexico (for locality and region locations see Fig. 1). Locus abbreviations are as follows: ADA, adenosine deaminase; GDH, glutamate dehydrogenase; GOT-2, glutamic oxalacetic transaminase-2; MPI, mannose phosphate isomerase; NP, nucleoside phosphorylase; 6-PGD, 6-phosphogluconate dehydrogenase; and PGM-2, phosphoglucomutase-2. Allele frequencies for prairie dogs from the different wards for four populations are also given. The common allele is designated as the "100" allele and additional alleles are numbered according to the mobility of their products relative to that of the common allele. Alleles not listed in the table are as follows: Ada-95, Gdh-92, Got-2-88, Mpi-105, Np-62, 6-Pgd-114, and 6-Pgd-122.

Region/Location	Number sampled	ADA	GDH	GOT-2	MPI	NP			6-PGD[1]	PGM-2		
		100	100	100	100	100	55	75	100	100	89	187
Clayton Region												
CAPU	60	1.00	.957	.814	.967	.775	.183	.042	.949	.833	.167	.000
ward 1	12	1.00	1.00	.917	1.00	.625	.292	.083	.958	.773	.227	.000
ward 2	22	1.00	.932	.786	.932	.841	.114	.045	.881	.800	.200	.000
ward 3	12	1.00	.955	1.00	.958	.833	.167	.000	1.00	.750	.250	.000
ward 4	14	1.00	.962	.607	1.00	.750	.214	.036	1.00	1.00	.000	.000
CLAY	16	.969	.906	.969	1.00	.938	.031	.031	.938	.875	.031	.094
ward 1	8	1.00	1.00	1.00	1.00	.938	.062	.000	1.00	.813	.000	.188
ward 2	8	.938	.813	.938	1.00	.938	.000	.062	.875	.938	.062	.000
HAYD	32	1.00	.781	.969	.938	.516	.078	.375	.906	.765	.103	.132
NAVI	18	1.00	.889	.750	.889	.111	.889	.000	.917	.583	.417	.000
SAJO	8	1.00	1.00	1.00	1.00	.500	.000	.500	.429	1.00	.000	.000

Table 1. Continued.

Region/Location	Number sampled	ADA	GDH	GOT-2	MPI	NP			6-PGD[1]	PGM-2		
		100	100	100	100	100	55	75	100	100	89	187
Roosevelt County Region												
MULE	18	.944	.778	.722	1.00	.694	.278	.028	.500	.889	.111	.000
BLAK	20	.925	1.00	.583	1.00	.550	.300	.150	.600	.875	.125	.000
PORT	113	.951	.879	.830	1.00	.858	.111	.027	.522	.782	.168	.050
ward 1	36	.933	1.00	.833	1.00	.867	.033	.100	.433	1.00	.000	.000
ward 2	29	1.00	.953	.969	1.00	.955	.045	.000	.559	.667	.303	.030
ward 3	15	.944	.861	.667	1.00	.875	.111	.014	.500	.758	.182	.061
ward 4	33	.914	.759	.879	1.00	.724	.224	.034	.552	.828	.086	.086
POR2	14	1.00	.821	.857	1.00	.571	.179	.250	.357	.929	.071	.000
POR3	15	1.00	.900	.867	1.00	.607	.143	.183	.700	.967	.033	.000
ward 1	8	1.00	.813	1.00	1.00	.611	.167	.167	.813	.938	.063	.000
ward 2	7	1.00	1.00	.714	1.00	.600	.100	.200	.571	1.00	.000	.000
POR4	7	1.00	.714	.714	1.00	.643	.357	.000	.571	.571	.429	.000
CAUS	14	1.00	.786	.583	1.00	.667	.167	.167	.818	.929	.071	.000
LING	15	1.00	1.00	1.00	1.00	.750	.036	.214	.667	.786	.214	.000
DORA	20	.950	.850	.850	1.00	.750	.250	.000	.650	.658	.342	.000
HYWY	23	.957	.717	.957	1.00	.870	.109	.022	.717	.833	.048	.119

Table 1. Continued.

Region/Location	Number sampled	ADA	GDH	GOT-2	MPI	NP			6-PGD[1]	PGM-2		
		100	100	100	100	100	55	75	100	100	89	187
HWY2	12	1.00	.708	.917	1.00	.917	.000	.083	.818	.958	.000	.042
MILN	28	.982	.714	.929	1.00	.704	.167	.130	.463	.800	.120	.080
Roswell Region												
ROS1	15	1.00	1.00	1.00	1.00	.800	.000	.200	.286	.714	.286	.000
ROS2	15	1.00	1.00	1.00	1.00	.700	.133	.167	.367	1.00	.000	.000
Tularosa Basin Region												
CARZ	25	.909	1.00	1.00	1.00	.413	.348	.239	.333	1.00	.000	.000
ALAM	21	1.00	.675	1.00	1.00	.905	.095	.000	.550	1.00	.000	.000

[1]6-Pgd-122 was present in the following populations: POR3, 0.200; POR3 ward 2, 0.429.

Table 2. Results of the analysis of F-statistics (Nei 1977) for each variable locus for black-tailed prairie dogs from populations within various regions in New Mexico (see text) and when data for animals from all regions were combined.

Localities	Locus[1]	F_{IT}	F_{IS}	F_{ST}	Chi square	Degrees of freedom
Clayton	ADA	.0276	.0000	.0276	7.3	4
Region	GDH	.4968	.4638	.0616	16.3***	4
(5 populations)	GOT-2	.4695	.4638	.0616	18.8***	4
	MPI	.6573	.6484	.0253	6.8	4
	NP	.4131	.1569	.3039	244.3***	12
	6-PGD	.3584	.2432	.1523	40.2***	4
	PGM-2	.4756	.4300	.0800	42.6***	8
	TOTAL	.4141	.3388	.1031	376.3***	40
Roosevelt	ADA	.1724	.1582	.0168	10.0	11
County	GDH	.4740	.4411	.0588	35.1***	11
Region	GOT-2	.3700	.3145	.0809	47.6***	11
(12 pops.)	NP	.1797	.1191	.0689	120.3***	33
	6-PGD	.1060	.0457	.0632	74.3***	22
	PGM-2	.4715	.4415	.0538	62.2***	22
	TOTAL	.2534	.2171	.0489	349.4***	110
Tularosa	ADA	.4875	.4625	.0466	3.4	1
Basin	GDH	.3864	.2222	.2100	18.4***	1
Region	NP	.4370	.3164	.1764	48.1***	2
(2 pops.)	6-PGD	.2272	.1185	.0476	3.9*	1
	TOTAL	.2197	.1700	.0688	73.8***	5

Table 2. Continued.

Localities	Locus	F_{IT}	F_{IS}	F_{ST}	Chi square	Degrees of freedom
Roswell	NP	.1842	.1738	.0127	2.3	2
Region	6-PGD	.3198	.3147	.0074	0.4	1
(2 pops.)	PGM-2	.4407	.3250	.1714	9.9***	1
	TOTAL	.3150	.2711	.0639	12.6*	4
All	ADA	.2226	.1917	.0318	31.2*	20
Regions	GDH	.4784	.4277	.0885	89.4***	20
(21 pops.)	GOT-2	.4143	.3451	.1056	106.3***	20
	MPI	.6687	.6484	.0577	58.0***	20
	NP	.2988	.1580	.1672	500.7***	60
	6-PGD	.2674	.0986	.1873	371.6***	40
	PGM-2	.4801	.4328	.0835	164.6***	40
	TOTAL	.4043	.3297	.1031	1322.6***	240

[1]Locus names are given in Table 1.

*P < 0.05; **P < 0.01; ***P < 0.001

Table 3. Results of the analysis of genetic differences among wards within four populations and among coteries within wards of the PORT population (Fig. 3). Values for the *F*-statistics are averages over all variable loci. Chi-square values and degrees of freedom were summed over those calculated for each locus. Coterie boundries were not determined for ward 4 of the PORT population.

Population units	F_{IT}	F_{IS}	F_{ST}	Chi square	Degrees of freedom
		Among Wards			
CAPU (4 wards)	.4614	.4327	.0554	47.0*	21
CLAY (2 wards)	.3163	.2943	.0446	12.4	8
POR3 (2 wards)	.1218	.0677	.0652	19.3*	8
PORT (4 wards)	.2631	.2248	.0541	111.8***	27
	Within Three Wards of PORT Population				
Ward 1 (5 coteries)	.1516	.0018	.1521	57.9*	40
Ward 2 (5 coteries)	.3067	.1600	.1830	53.1***	28
Ward 3 (8 coteries)	.3207	.1408	.2164	110.2***	56
Combined (8 coteries)	.3079	.1123	.2274	264.3***	144

*P < 0.05; **P < 0.01; ***P < 0.001

Table 4. Results of the analysis of gene diversity (Nei 1973, 1975) for each variable locus for black-tailed prairie dogs from different hierarchial levels; wards (*W*), populations (*P*), and regions (*R*) within the total (*T*) across all populations. The values for each locus and the mean over all loci represent the amount of gene differentiation accounted for by the various hierarchial levels; wards within populations (G_{WP}), wards within regions (G_{WR}), wards within the total (G_{WT}), populations within regions (G_{PR}), populations within the total (G_{PT}), and regions within the total (G_{RT}).

Locus[1]	G_{WP}	G_{WR}	G_{WT}	G_{PR}	G_{PT}	G_{RT}
ADA	.0113	.0329	.0428	.0218	.0318	.0102
GDH	.0214	.0940	.1018	.0742	.0885	.0155
GOT-2	.0605	.1340	.1598	.0782	.1056	.0297
MPI	.0101	.0352	.0673	.0253	.0577	.0332
NP	.0127	.1638	.1772	.1531	.1672	.0161
6-PGD	.0101	.0775	.1955	.0681	.1873	.1279
PGM-2	.0295	.0954	.1105	.0679	.0835	.0167
MEAN	.0222	.0904	.1221	.0698	.1031	.0356

[1]Locus names are given in Table 1.

Figure 1. Map of collecting localities of black-tailed prairie dogs in New Mexico. The Roosevelt County region has been expanded to clearly depict spatial relationships among the locations.

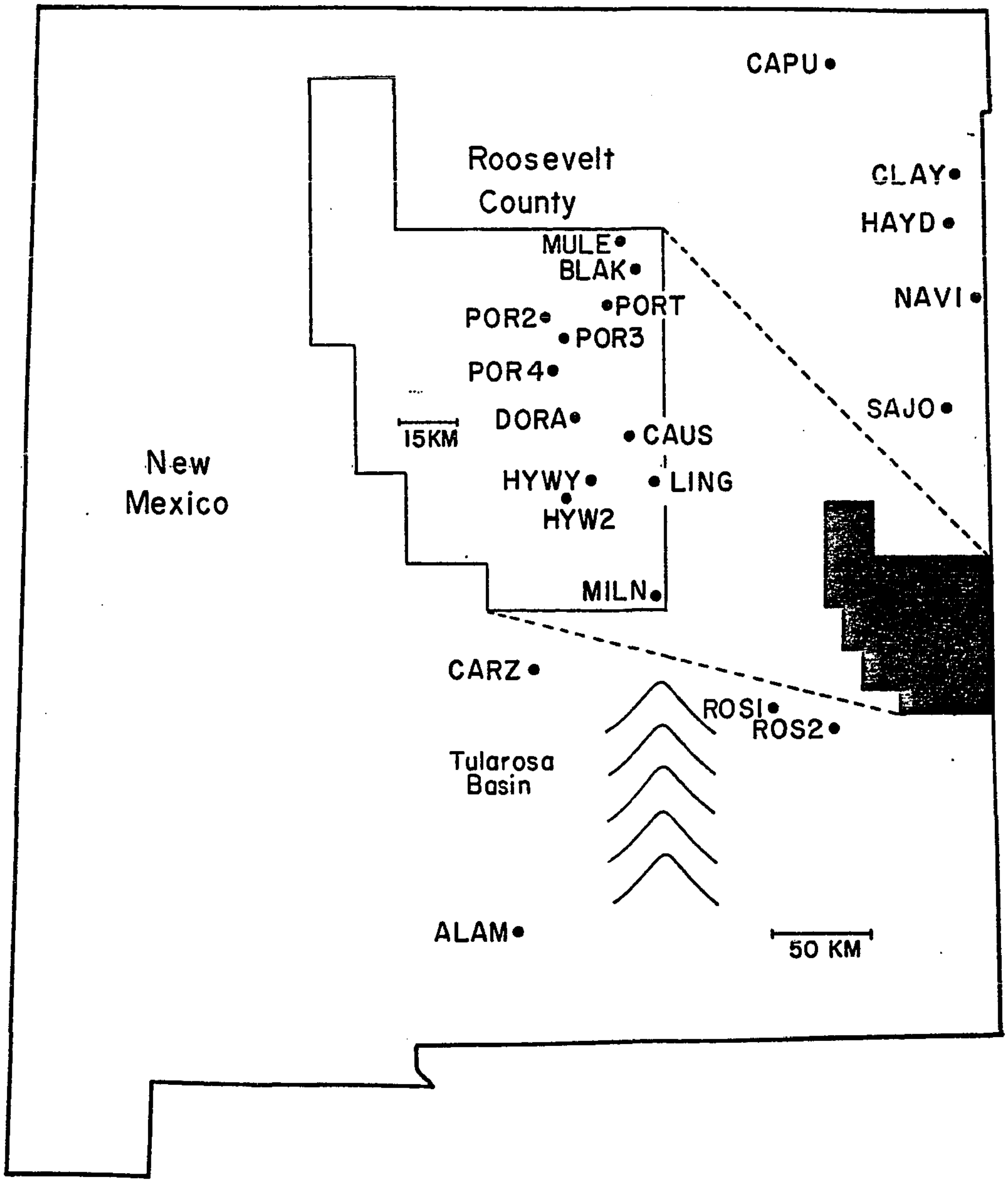

CAPU
Roosevelt County
CLAY
HAYD
MULE
BLAK
PORT
NAVI
POR2
POR3
POR4
SAJO
DORA
CAUS
15KM
New Mexico
HYWY
LING
HYW2
MILN
CARZ
ROS1
ROS2
Tularosa Basin
ALAM
50 KM

Figure 2. Dendrogram (UPGMA) of genetic identities (*I*; Nei 1972), between populations of black-tailed prairie dogs from 21 collecting locations in New Mexico. Locations of populations are shown in Fig. 1.

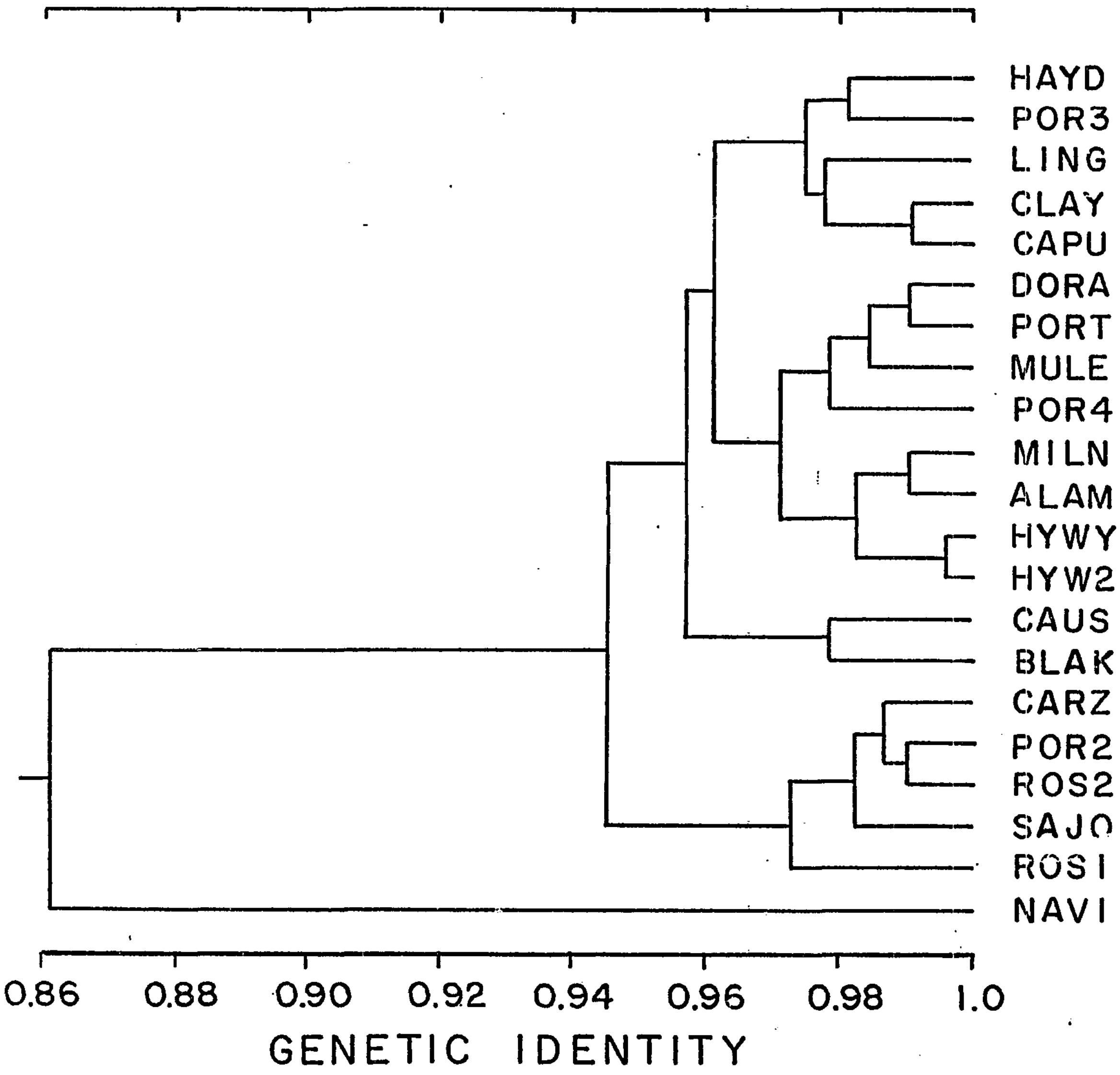
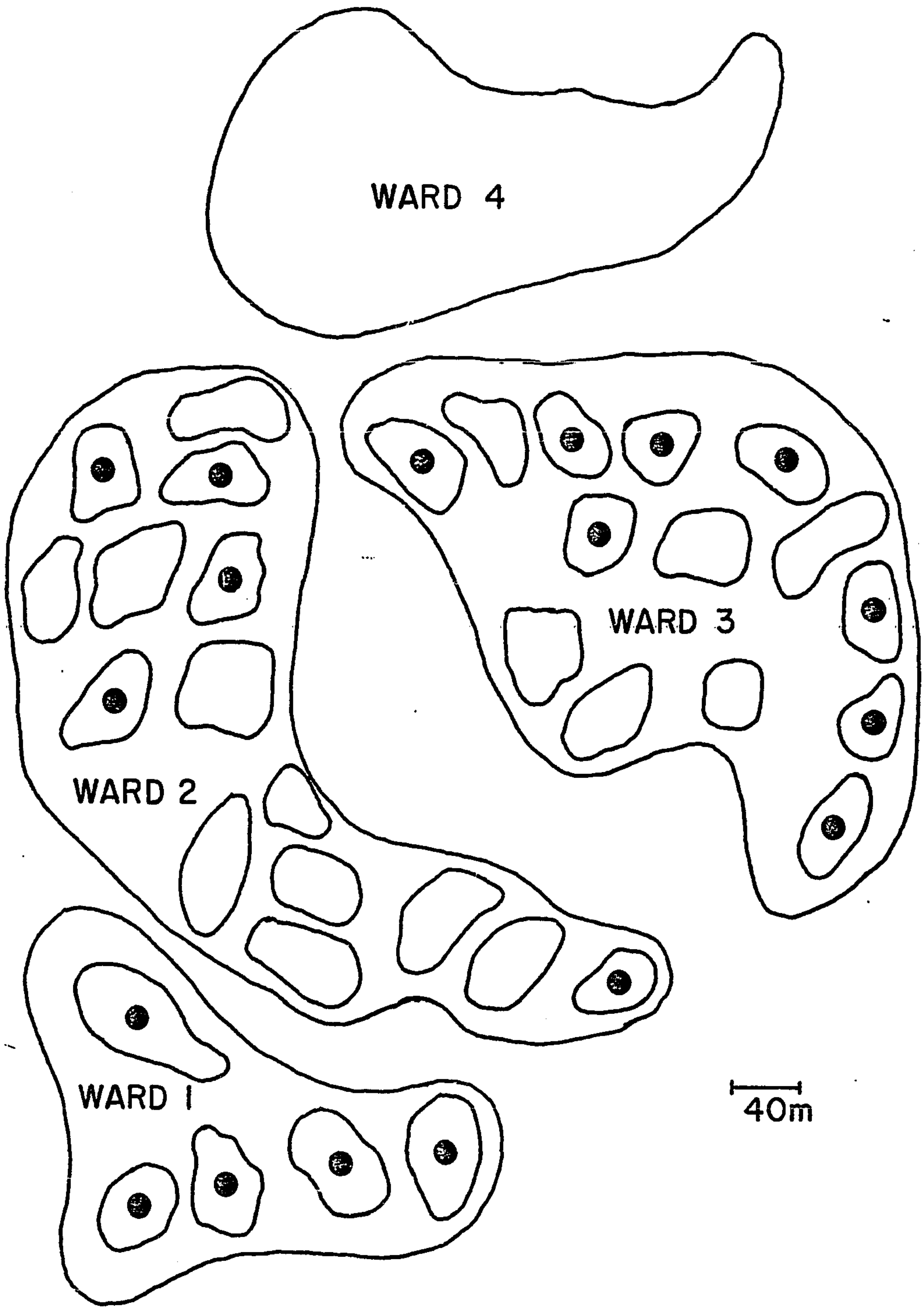

HAYD
POR3
LING
CLAY
CAPU
DORA
PORT
MULE
POR4
MILN
ALAM
HYWY
HYW2
CAUS
BLAK
CARZ
POR2
ROS2
SAJO
ROS1
NAVI
0.86
0.88
0.90
0.92
0.94
0.96
0.98
1.0
GENETIC IDENTITY

Figure 3. Ward and coterie boundries within the PORT population of black-tailed prairie dogs. The dots indicate coteries where three or more prairie dogs were collected. Coterie boundaries were not determined within ward 4.


WARD 4
WARD 3
WARD 2
WARD 1
40m

CRANIAL VARIATION AMONG POPULATIONS OF THE

BLACK-TAILED PRAIRIE DOG IN NEW MEXICO

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ABSTRACT.-Variation of 17 cranial measurements for 188 adult male and 130 adult female black-tailed prairie dogs (Cynomys ludovicianus) from 18 localities in New Mexico was assessed. Fifteen of the 17 measurements showed significant sexual dimorphism with males larger in each case. Most characters showed significant interlocality variation although no geographic trends were apparent. The results were not consistent with previous taxonomic treatments of this species within the study region. Phenetic relationships between samples were not significantly associated with those reported earlier for electrophoretic data. However, the amount of morphometric variability accounted for by differences among samples within four physiographic regions and that among the regions were virtually identical to the amount measured by electrophoretic data. Variation among samples separated by short geographic distances (< 15 km) was often greater than that among populations from widely separated regions. Difficulties associated with classical methods of systematic classification for species with disjunct patterns of variability are discussed.

Taxonomic relationships among populations have classically been derived from comparisons of skeletal morphology (Hall and Kelson, 1959; Sneath and Sokal, 1973). Populations of the same species which are similar in their morphometric traits and are 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 their alleged direct competition with livestock for forage and with agriculture for potential croplands, the prairie dog has been subject to attempted erradication 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 for the animals from the Tularosa Basin. Since prairie dogs were rare in that region, he classified them as endangered. However, I (Chesser, 1981) found that genetic heterogeneity among populations of prairie dogs in New Mexico is high even when compared over relatively short geographic distances; the genetic findings did not support previous taxonomic classifications of this species. The amount of differentiation among local populations was 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. However, studies which concentrate on differences over large geographic distances may essentially ignore the possibility of heterogeneity over limited space. The isolation of prairie dog populations by man-caused and natural factors may enhance heterogeneity over short distances. My purpose was to examine the variation of cranial dimensions of black-tailed prairie dogs from populations separated by short and by long geographic distances in New Mexico. Statistical methods will be 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 as in Chesser (1981) as being from one of four regions separated by major geological formations: (1) the Clayton region is north of the bluffs of the Llano Estacado; (2) the Roosevelt County region is on the Llano Estacado; (3) the Roswell region is on the premontane alluvial plain; and (4) the Tularosa Basin region is situated to the west of the Capitan Mountains.

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 crainial 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 interlocality differentiation and sexual dimorphism of cranial dimensions. 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 standarized 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 were analyzed by variance components analysis (c.f. Straney, 1976). Associations between matrices of phenetic distance and linear distance between localities 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 ($P < 0.001$). Pizzamenti (1975) reported that prairie dogs were slightly to moderately sexually dimorphic and chose to combine measurements for the two sexes in subsequent analyses (Pizzamenti, 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, $t_{\infty}=2.02$, $\underline{P}<0.05$; 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 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. 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 which reflected the overall size of the skull. Internal 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 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 nor those from the nearby Roswell region (ROS1 and ROS2). Neither morpholgical nor genetic 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. Prairie dogs are rare in that region and the two populations sampled (ALAM and CARZ) were the only ones of any significant size that I was able to locate. Disease or indiscriminant poisoning could quickly eliminate prairie dogs from this region of New Mexico. Subsequent reintroduction of prairie dogs into the region could result in substantial modification of the present morphological characteristics. The strong variation among local populations poses some unique logistical problems for programs whose goals are to protect unique and threatened organisms. The Tularosa Basin prairie dogs do not meet the criterea of a separate subspecies 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 protection of rare populations of prairie dogs. The first would be to designate a large number of subspecies of prairie dogs many of which would be endangered. The second and more tenable option is to lump them all as a single subspecies and rely on local organizations to ensure the protection of threatened prairie dog populations on a regional basis.

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 either samples compared within regions or between the 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 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 ($\underline{P} > 0.30$ for both males and females; $\underline{P} > 0.20$ when data for males and females were combined). Thus, as was 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. Stochas[illegible]nd/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 my (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 yrs 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). The high degree of variation among nearby samples makes the identification of variables that would characterize distinct subspecific groups difficult.

The arguments above 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. 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 species and differing taxonomically from other populations of the species" [Mayr, 1963 p. 210]) is probably not applicable to prairie dogs.
The 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.

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Table 1. Collection localities of black-tailed prairie dogs in New Mexico (NM). Sample abbreviations and regions refer to those depicted in Fig. 1A.

Clayton Region

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

Roosevelt County Region

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

Roswell Region

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

Tularosa Basin Region

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

Table 2. Mean values (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

Table 2. Continued.

Character	Sex	Mean	F ratio	Principal components		
				I	II	III
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.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

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		
	Location	Region	Within locations	Location	Region	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

Table 3. Continued.

Skull character	Males: Location	Males: Region	Males: Within locations	Females: Location	Females: Region	Females: Within locations
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

Figure 1. Map of collecting localities for black-tailed prairie dogs in New Mexico (A), and three-dimensional models depicting of relationships among samples for male (B) and female (C) prairie dogs. The models were derived by principal components analysis using 17 cranial characters.

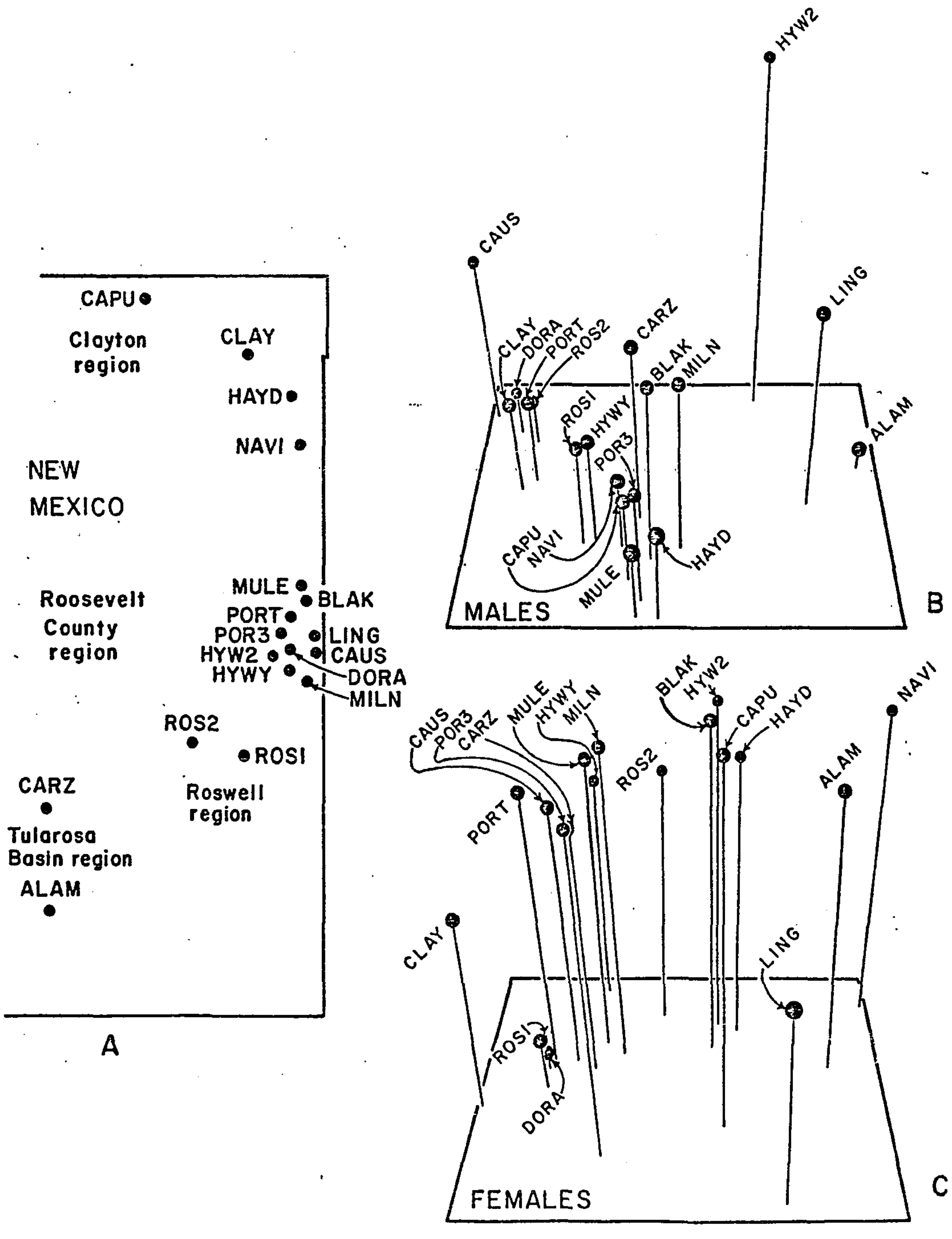
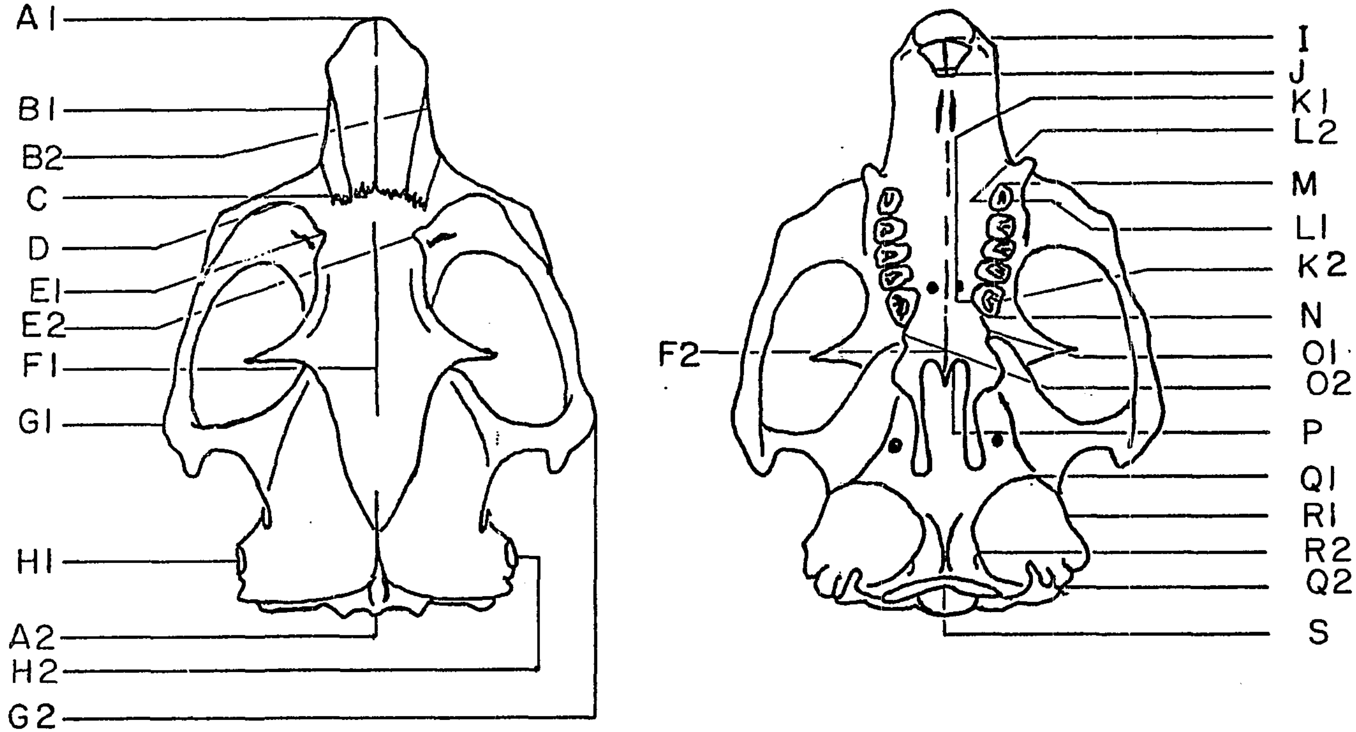

CAPU
Clayton region
CLAY
HAYD
NAVI
NEW MEXICO
Roosevelt County region
MULE
BLAK
PORT
POR3
LING
HYW2
CAUS
HYWY
DORA
MILN
ROS2
ROS1
CARZ
Roswell region
Tularosa Basin region
ALAM
A
HYW2
CAUS
LING
CLAY
DORA
PORT
ROS2
CARZ
BLAK
MILN
ROS1
HYWY
ALAM
POR3
CAPU
NAVI
MULE
HAYD
MALES
B
BLAK
HYW2
CAPU
HAYD
NAVI
CAUS
POR3
CARZ
MULE
HYWY
MILN
ROS2
ALAM
PORT
CLAY
LING
ROS1
DORA
FEMALES
C

Figure 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 (O1-O2); 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).


A1
B1
B2
C
D
E1
E2
F1
G1
H1
A2
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G2
F2
I
J
K1
L2
M
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Q2
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APPENDICES

Appendix I. Mean, standard error, variance, coefficient of variation (C.V.) and sample size (N) for 17 cranial measurements of adult black-tailed prairie dogs of each sex from 18 locations in New Mexico. Location abbreviations are as in Fig. 1 of the previous paper. Skull measurements are as follows: total length (TLTH); basalar length (BASL); rostral length (ROSL); nasal length (NASL); upper diastemal length (DIAST); maxillary toothrow length (TOROW); palatine width (PALW); rostral width (ROSW); width of the third molar (MOL3); first premolar width (PREM); postpalatal length (POPAL); auditory bulla length (BULL); auditory bulla width (BULW); greatest width of skull (WIDG); mastoid breadth (WID2); greatest width of skull (WIDG); mastoid breadth (WID2); least interorbital width (CONS); and skull depth (DEPT).

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
LOCATION=ALAM SEX=FEMALE					
TLTH	8	6.28000000	0.04610741	0.01700714	2.077
BASL	8	5.69625000	0.05458242	0.02383393	2.710
ROSL	8	2.60875000	0.03662978	0.01073393	3.971
NASL	8	2.41937500	0.03476243	0.00966741	4.064
DIAST	8	1.50375000	0.01569093	0.00196964	2.951
TOROW	8	1.56750000	0.01592393	0.00202857	2.873
PALW	8	0.91062500	0.01023987	0.00083884	3.181
ROSW	8	1.16875000	0.01305038	0.00136250	3.158
MOL3	8	0.45125000	0.01371749	0.00150536	8.598
PREM	8	0.31625000	0.00337401	0.00009107	3.018
POPAL	8	2.24375000	0.03231748	0.00835536	4.074
BULL	8	1.14812500	0.01639189	0.00214955	4.038
BULW	8	1.09437500	0.02398730	0.00460312	6.200
WIDG	8	4.43937500	0.02849557	0.00649598	1.816
WID2	8	2.75250000	0.04552276	0.01657857	4.678
CONS	8	1.27562500	0.02481067	0.00492455	5.501
DEPT	8	1.84250000	0.02218027	0.00393571	3.405

LOCATION=ALAM SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	13	6.49923077	0.04890089	0.03108686	2.713
BASL	13	5.87500000	0.05224756	0.03548750	3.206
ROSL	13	2.70038462	0.02372020	0.00731442	3.167
NASL	13	2.48000000	0.03312757	0.01426667	4.816
DIAST	13	1.58192308	0.02067405	0.00555641	4.712
TOROW	13	1.59346154	0.01010180	0.00132660	2.286
PALW	13	0.90461538	0.01366332	0.00242692	5.446
ROSW	13	1.21730769	0.01664693	0.00360256	4.931
MOL3	13	0.46230769	0.01322410	0.00227340	10.314
PREM	13	0.32230769	0.00833235	0.00090256	9.321
POPAL	13	2.31653846	0.03797935	0.01875160	5.911
BULL	13	1.17076923	0.01715172	0.00382436	5.282
BULW	13	1.09923077	0.01669721	0.00362436	5.477
WIDG	13	4.63423077	0.04388156	0.02503269	3.414
WID2	13	2.81961538	0.03050043	0.01209359	3.900
CONS	13	1.37269231	0.04760150	0.02945673	12.503
DEPT	13	1.92769231	0.02573045	0.00860673	4.813

----------------------- LOCATION=BLAK SEX=FEMALE -----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	6	6.17166667	0.05535742	0.01838667	2.197
BASL	6	5.55000000	0.06403124	0.02460000	2.826
ROSL	6	2.57416667	0.05091523	0.01555417	4.845
NASL	6	2.37416667	0.04444878	0.01185417	4.586
DIAST	6	1.39583333	0.01781463	0.00190417	3.126
TOROW	6	1.63750000	0.01641899	0.00161750	2.456
PALW	6	0.86000000	0.02217356	0.00295000	6.316
ROSW	6	1.08833333	0.01458690	0.00127667	3.283
MOL3	6	0.37083333	0.00506897	0.00015417	3.348
PREM	6	0.31666667	0.00477261	0.00013667	3.692
POPAL	6	2.16333333	0.01842402	0.00203667	2.086
BULL	6	1.08666667	0.02713137	0.00441667	6.116
BULW	6	1.00916667	0.01800077	0.00194417	4.369
WIDG	6	4.33416667	0.06482562	0.02521417	3.664
WID2	6	2.70416667	0.06381505	0.02443417	5.780
CONS	6	1.27833333	0.01994437	0.00238667	3.822
DEPT	6	1.87583333	0.02800050	0.00470417	3.656

LOCATION=BLAK SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	8	6.28687500	0.07295998	0.04258527	3.282
BASL	8	5.62562500	0.07954355	0.05061741	3.999
ROSL	8	2.66750000	0.04808846	0.01850000	5.099
NASL	8	2.43312500	0.03464021	0.00959955	4.027
DIAST	8	1.40062500	0.02457564	0.00483170	4.963
TOROW	8	1.64437500	0.01740888	0.00242455	2.994
PALW	8	0.88437500	0.01151232	0.00106027	3.682
ROSW	8	1.11562500	0.01686177	0.00227455	4.275
MOL3	8	0.39187500	0.00828820	0.00054955	5.982
PREM	8	0.31812500	0.00388880	0.00012098	3.458
POPAL	8	2.21750000	0.04497023	0.01617857	5.736
BULL	8	1.12500000	0.02743499	0.00602143	6.898
BULW	8	1.02937500	0.01881388	0.00283170	5.170
WIDG	8	4.42375000	0.04923296	0.01939107	3.148
WID2	8	2.72187500	0.04749941	0.01804955	4.936
CONS	8	1.36812500	0.05386771	0.02321384	11.136
DEPT	8	1.93875000	0.01933608	0.00299107	2.821

---------------------- LOCATION=CAPU SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	9	6.20111111	0.04935541	0.02192361	2.388
BASL	9	5.51611111	0.05480887	0.02703611	2.981
ROSL	9	2.60555556	0.02707300	0.00659653	3.117
NASL	9	2.31611111	0.01533826	0.00211736	1.987
DIAST	9	1.37111111	0.03621673	0.01180486	7.924
TOROW	9	1.58166667	0.05896680	0.03129375	11.184
PALW	9	0.87277778	0.01607515	0.00232569	5.526
ROSW	9	1.12333333	0.01611590	0.00233750	4.304
MOL3	9	0.39111111	0.01682792	0.00254861	12.908
PREM	9	0.31777778	0.00578018	0.00030069	5.457
POPAL	9	2.17388889	0.02701309	0.00656736	3.728
BULL	9	1.07777778	0.01152025	0.00119444	3.207
BULW	9	1.01777778	0.01453232	0.00190069	4.284
WIDG	9	4.49000000	0.05291503	0.02520000	3.536
WID2	9	2.68666667	0.02643125	0.00628750	2.951
CONS	9	1.24611111	0.04062684	0.01485486	9.781
DEPT	9	1.90555556	0.01162028	0.00121528	1.829

LOCATION=CAPU SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	20	6.30425000	0.04801490	0.04610862	3.406
BASL	20	5.62025000	0.04859401	0.04722757	3.867
ROSL	20	2.63875000	0.02342927	0.01097862	3.971
NASL	20	2.36050000	0.01844230	0.00680237	3.494
DIAST	20	1.40200000	0.01975641	0.00780632	6.302
TOROW	20	1.62655000	0.00828330	0.00137226	2.277
PALW	20	0.87600000	0.00686908	0.00094368	3.507
ROSW	20	1.13075000	0.01231855	0.00303493	4.872
MOL3	20	0.38325000	0.00909941	0.00165599	10.618
PREM	20	0.31825000	0.00437209	0.00038230	6.144
POPAL	20	2.23275000	0.03230096	0.02086704	6.470
BULL	20	1.12200000	0.01732582	0.00600368	6.906
BULW	20	1.02200000	0.01285752	0.00330632	5.626
WIDG	20	4.50450000	0.04271986	0.03649974	4.241
WID2	20	2.74325000	0.02318766	0.01075336	3.780
CONS	20	1.29275000	0.02177177	0.00948020	7.532
DEPT	20	1.93000000	0.01440943	0.00415263	3.339

---------------------- LOCATION=CARZ SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	11	6.01454545	0.03789012	0.01579227	2.089
BASL	11	5.36727273	0.02852721	0.00895182	1.763
ROSL	11	2.53954545	0.02274817	0.00569227	2.971
NASL	11	2.24181818	0.03143733	0.01087136	4.651
DIAST	11	1.36045455	0.02029839	0.00453227	4.949
TOROW	11	1.59272727	0.01081539	0.00128682	2.252
PALW	11	0.87363636	0.00965521	0.00102545	3.665
ROSW	11	1.10045455	0.07410206	0.06040227	22.333
MOL3	11	0.36954545	0.00702122	0.00054227	6.301
PREM	11	0.29681818	0.00245623	0.00006636	2.745
POPAL	11	2.11272727	0.02415258	0.00641682	3.792
BULL	11	1.13954545	0.01193647	0.00156727	3.474
BULW	11	0.99227273	0.02099095	0.00484682	7.016
WIDG	11	4.19909091	0.03004404	0.00992909	2.373
WID2	11	2.58409091	0.02586519	0.00735909	3.320
CONS	11	1.20318182	0.01331904	0.00195136	3.671
DEPT	11	1.82590909	0.01641532	0.00296409	2.982

LOCATION=CARZ SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	11	6.31818182	0.06745124	0.05004636	3.541
BASL	11	5.71636364	0.06275526	0.04332045	3.641
ROSL	11	2.65227273	0.03860855	0.01639682	4.828
NASL	11	2.41954545	0.03600792	0.01426227	4.936
DIAST	11	1.47454545	0.03116273	0.01068227	7.009
TOROW	11	1.61363636	0.01089393	0.00130545	2.239
PALW	11	0.89818182	0.01158511	0.00147636	4.278
ROSW	11	1.12409091	0.01903129	0.00398409	5.615
MOL3	11	0.42181818	0.01340408	0.00197636	10.539
PREM	11	0.31181818	0.00463547	0.00023636	4.930
POPAL	11	2.26318182	0.02484747	0.00679136	3.641
BULL	11	1.17636364	0.01700389	0.00318045	4.794
BULW	11	1.02954545	0.01976515	0.00429727	6.367
WIDG	11	4.45863636	0.03927809	0.01697045	2.922
WID2	11	2.68954545	0.02893138	0.00920727	3.568
CONS	11	1.31863636	0.02690971	0.00796545	6.768
DEPT	11	1.91727273	0.01299237	0.00185682	2.248

---------------------- LOCATION=CAUS SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	5.98500000	0.03547299	0.00377500	1.027
BASL	3	5.32333333	0.07886345	0.01865833	2.566
ROSL	3	2.53666667	0.02455153	0.00180833	1.676
NASL	3	2.23666667	0.03320810	0.00330833	2.572
DIAST	3	1.37500000	0.03214550	0.00310000	4.049
TOROW	3	1.58000000	0.05299371	0.00842500	5.809
PALW	3	0.91666667	0.05696002	0.00973333	10.763
ROSW	3	1.35333333	0.24087226	0.17405833	30.828
MOL3	3	0.39000000	0.00500000	0.00007500	2.221
PREM	3	0.31166667	0.00166667	0.00000833	0.926
POPAL	3	2.14000000	0.05267827	0.00832500	4.264
BULL	3	1.13833333	0.00833333	0.00020833	1.268
BULW	3	0.98333333	0.04146618	0.00515833	7.304
WIDG	3	4.17333333	0.06647890	0.01325833	2.759
WID2	3	2.53333333	0.05456902	0.00893333	3.731
CONS	3	1.27500000	0.07571878	0.01720000	10.286
DEPT	3	1.88833333	0.03443996	0.00355833	3.159

LOCATION=CAUS SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	6.05333333	0.02315407	0.00160833	0.663
BASL	3	5.46000000	0.05000000	0.00750000	1.586
ROSL	3	2.55000000	0.03000000	0.00270000	2.038
NASL	3	2.36166667	0.05674015	0.00965833	4.161
DIAST	3	1.36000000	0.00866025	0.00022500	1.103
TOROW	3	1.61333333	0.02048034	0.00125833	2.199
PALW	3	0.88000000	0.04000000	0.00480000	7.873
ROSW	3	1.08000000	0.04041452	0.00490000	6.481
MOL3	3	0.38666667	0.00726483	0.00015833	3.254
PREM	3	0.30333333	0.00600925	0.00010833	3.431
POPAL	3	2.22166667	0.11980308	0.04305833	9.340
BULL	3	1.17666667	0.00927961	0.00025833	1.366
BULW	3	0.96000000	0.01527525	0.00070000	2.756
WIDG	3	4.30333333	0.02962731	0.00263333	1.192
WID2	3	2.63000000	0.01527525	0.00070000	1.006
CONS	3	1.41000000	0.02000000	0.00120000	2.457
DEPT	3	1.86500000	0.01258306	0.00047500	1.169

LOCATION=CLAY SEX=FEMALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	11	6.17272727	0.05697433	0.03570682	3.061
BASL	11	5.56681818	0.06397540	0.04502136	3.812
ROSL	11	2.57181818	0.03774479	0.01567136	4.868
NASL	11	2.27318182	0.03668213	0.01480136	5.352
DIAST	11	1.37590909	0.02233849	0.00548909	5.385
TOROW	11	1.64227273	0.01160650	0.00148182	2.344
PALW	11	0.89181818	0.01292061	0.00183636	4.805
ROSW	11	1.12181818	0.01821928	0.00365136	5.386
MOL3	11	0.38409091	0.00471064	0.00024409	4.068
PREM	11	0.30636364	0.00447675	0.00022045	4.846
POPAL	11	2.21818182	0.03473453	0.01327136	5.194
BULL	11	1.13000000	0.01720201	0.00325500	5.049
BULW	11	1.04909091	0.02175084	0.00520409	6.876
WIDG	11	4.40545455	0.06051467	0.04028227	4.556
WID2	11	2.71409091	0.02992277	0.00984909	3.657
CONS	11	1.33181818	0.02792256	0.00857636	6.954
DEPT	11	1.88363636	0.01728229	0.00328545	3.043

LOCATION=CLAY SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	20	6.26375000	0.03535325	0.02499704	2.524
BASL	20	5.67925000	0.03789229	0.02871651	2.984
ROSL	20	2.61325000	0.01671461	0.00558757	2.860
NASL	20	2.33525000	0.02337755	0.01093020	4.477
DIAST	20	1.39875000	0.01375000	0.00378125	4.396
TOROW	20	1.67550000	0.00646753	0.00083658	1.726
PALW	20	0.89650000	0.00837525	0.00140289	4.178
ROSW	20	1.12550000	0.01233256	0.00304184	4.900
MOL3	20	0.38200000	0.00394702	0.00031158	4.621
PREM	20	0.32175000	0.00241364	0.00011651	3.355
POPAL	20	2.28675000	0.01920894	0.00737967	3.757
BULL	20	1.13150000	0.00890077	0.00158447	3.518
BULW	20	1.08075000	0.01279533	0.00327441	5.295
WIDG	20	4.50500000	0.02850900	0.01625526	2.830
WID2	20	2.76975000	0.01650548	0.00544862	2.665
CONS	20	1.30925000	0.01548885	0.00479809	5.291
DEPT	20	1.92900000	0.01300101	0.00338053	3.014

---------------------- LOCATION=DORA SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	4	5.95500000	0.07373941	0.02175000	2.477
BASL	4	5.31625000	0.03312697	0.00438958	1.246
ROSL	4	2.47125000	0.04190142	0.00702292	3.391
NASL	4	2.25250000	0.04575751	0.00837500	4.063
DIAST	4	1.32625000	0.00554339	0.00012292	0.836
TOROW	4	1.65125000	0.02125000	0.00180625	2.574
PALW	4	0.85375000	0.02409832	0.00232292	5.645
ROSW	4	1.10000000	0.01683251	0.00113333	3.060
MOL3	4	0.34750000	0.01108678	0.00049167	6.381
PREM	4	0.30750000	0.00661438	0.00017500	4.302
POPAL	4	2.09750000	0.02817357	0.00317500	2.686
BULL	4	1.08250000	0.00520416	0.00010833	0.962
BULW	4	0.95625000	0.02903841	0.00337292	6.073
WIDG	4	4.19375000	0.02625000	0.00275625	1.252
WID2	4	2.59750000	0.01761865	0.00124167	1.357
CONS	4	1.24750000	0.00853913	0.00029167	1.369
DEPT	4	1.79750000	0.00968246	0.00037500	1.077

LOCATION=DORA SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	7	6.12928571	0.12774337	0.11422857	5.514
BASL	7	5.51071429	0.13154045	0.12112024	6.315
ROSL	7	2.54428571	0.07092441	0.03521190	7.375
NASL	7	2.38000000	0.03580702	0.00897500	3.981
DIAST	7	1.44285714	0.04111333	0.01183214	7.539
TOROW	7	1.60857143	0.02164965	0.00328095	3.561
PALW	7	0.88071429	0.02223866	0.00346190	6.681
ROSW	7	1.08285714	0.05011721	0.01758214	12.245
MOL3	7	0.39428571	0.02356421	0.00388690	15.812
PREM	7	0.31357143	0.00998298	0.00069762	8.423
POPAL	7	2.20000000	0.07618899	0.04063333	9.163
BULL	7	1.15214286	0.03054772	0.00653214	7.015
BULW	7	1.05285714	0.01515229	0.00160714	3.808
WIDG	7	4.33571429	0.11097205	0.08620357	6.772
WID2	7	2.68500000	0.04678980	0.01532500	4.611
CONS	7	1.30357143	0.04042504	0.01143929	8.205
DEPT	7	1.83214286	0.03064499	0.00657381	4.425

---------------------- LOCATION=HAYD SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	4	5.87500000	0.14357054	0.08245000	4.888
BASL	4	5.24000000	0.20257715	0.16415000	7.732
ROSL	4	2.41625000	0.07872354	0.02478958	6.516
NASL	4	2.19375000	0.10046506	0.04037292	9.159
DIAST	4	1.28375000	0.05328285	0.01135625	8.301
TOROW	4	1.57875000	0.05636100	0.01270625	7.140
PALW	4	0.87750000	0.01127312	0.00050833	2.569
ROSW	4	1.07250000	0.02933286	0.00344167	5.470
MOL3	4	0.38000000	0.01837117	0.00135000	9.669
PREM	4	0.27625000	0.03454315	0.00477292	25.009
POPAL	4	2.07875000	0.09912902	0.03930625	9.537
BULL	4	1.07125000	0.02294695	0.00210625	4.284
BULW	4	0.94750000	0.05603198	0.01255833	11.827
WIDG	4	4.11125000	0.18625000	0.13875625	9.061
WID2	4	2.57000000	0.08553752	0.02926667	6.657
CONS	4	1.17250000	0.06179604	0.01527500	10.541
DEPT	4	1.89625000	0.03210497	0.00412292	3.386

LOCATION=HAYD SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	7	6.18357143	0.10618781	0.07893095	4.543
BASL	7	5.53857143	0.11111831	0.08643095	5.308
ROSL	7	2.59214286	0.05098853	0.01819881	5.204
NASL	7	2.35571429	0.07080682	0.03509524	7.952
DIAST	7	1.39571429	0.04712482	0.01554524	8.933
TOROW	7	1.60571429	0.02088599	0.00305357	3.441
PALW	7	0.91714286	0.01204442	0.00101548	3.475
ROSW	7	1.12357143	0.02663050	0.00496429	6.271
MOL3	7	0.38142857	0.01298874	0.00118095	9.010
PREM	7	0.32285714	0.01016865	0.00072381	8.333
POPAL	7	2.20142857	0.07066617	0.03495595	8.493
BULL	7	1.10928571	0.02318221	0.00376190	5.529
BULW	7	0.99785714	0.02225012	0.00346548	5.899
WIDG	7	4.23000000	0.09382735	0.06162500	5.869
WID2	7	2.63500000	0.04051749	0.01149167	4.068
CONS	7	1.28285714	0.06694754	0.03137381	13.807
DEPT	7	1.91428571	0.02527064	0.00447024	3.493

----------------------- LOCATION=HYWY SEX=FEMALE -----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	6.03833333	0.08516324	0.02175833	2.443
BASL	3	5.39666667	0.11292820	0.03825833	3.624
ROSL	3	2.53166667	0.03919325	0.00460833	2.681
NASL	3	2.21500000	0.13967224	0.05852500	10.922
DIAST	3	1.36333333	0.04437842	0.00590833	5.638
TOROW	3	1.60833333	0.02420973	0.00175833	2.607
PALW	3	0.87333333	0.00333333	0.00003333	0.661
ROSW	3	1.13000000	0.01322876	0.00052500	2.028
MOL3	3	0.36333333	0.00726483	0.00015833	3.463
PREM	3	0.31500000	0.01258306	0.00047500	6.919
POPAL	3	2.07666667	0.06359595	0.01213333	5.304
BULL	3	1.15000000	0.01527525	0.00070000	2.301
BULW	3	1.05000000	0.04509250	0.00610000	7.438
WIDG	3	4.23666667	0.06220486	0.01160833	2.543
WID2	3	2.67333333	0.07881060	0.01863333	5.106
CONS	3	1.39500000	0.00288675	0.00002500	0.358
DEPT	3	1.85500000	0.01607275	0.00077500	1.501

LOCATION=HYWY SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	9	6.25666667	0.06409086	0.03696875	3.073
BASL	9	5.59833333	0.08052346	0.05835625	4.315
ROSL	9	2.61666667	0.03042523	0.00833125	3.488
NASL	9	2.35000000	0.03847799	0.01332500	4.912
DIAST	9	1.37388889	0.03349728	0.01009861	7.314
TOROW	9	1.62722222	0.01387221	0.00173194	2.558
PALW	9	0.83055556	0.01321417	0.00157153	4.773
ROSW	9	1.14222222	0.02752664	0.00681944	7.230
MOL3	9	0.39277778	0.01341411	0.00161944	10.246
PREM	9	0.32111111	0.00498454	0.00022361	4.657
POPAL	9	2.23277778	0.04562156	0.01873194	6.130
BULL	9	1.14166667	0.01994785	0.00358125	5.242
BULW	9	1.04944444	0.02590641	0.00604028	7.406
WIDG	9	4.41422222	0.06969313	0.04371419	4.736
WID2	9	2.71111111	0.02850168	0.00731111	3.154
CONS	9	1.31555556	0.03905520	0.01372778	8.906
DEPT	9	1.90166667	0.01952562	0.00343125	3.080

---------------------- LOCATION=HYW2 SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	4	6.23125000	0.08792457	0.03092292	2.822
BASL	4	5.45375000	0.22314397	0.19917292	8.183
ROSL	4	2.56750000	0.07192299	0.02069167	5.603
NASL	4	2.44625000	0.06808007	0.01853958	5.566
DIAST	4	1.46375000	0.03043949	0.00370625	4.159
TOROW	4	1.38750000	0.14292335	0.08170833	20.602
PALW	4	0.86750000	0.01963203	0.00154167	4.526
ROSW	4	1.17000000	0.00645497	0.00016667	1.103
MOL3	4	0.41250000	0.00629153	0.00015833	3.050
PREM	4	0.30875000	0.00239357	0.00002292	1.550
POPAL	4	2.31875000	0.03037097	0.00368958	2.620
BULL	4	1.11625000	0.01048312	0.00043958	1.878
BULW	4	1.06500000	0.00707107	0.00020000	1.328
WIDG	4	4.50875000	0.11360339	0.05162292	5.039
WID2	4	2.51250000	0.15627833	0.09769167	12.440
CONS	4	1.15875000	0.11648274	0.05427292	20.105
DEPT	4	1.90875000	0.03016448	0.00363958	3.161

LOCATION=HYW2 SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	6.42166667	0.08709828	0.02275833	2.349
BASL	3	5.78000000	0.08736895	0.02290000	2.618
ROSL	3	2.67666667	0.01763834	0.00093333	1.141
NASL	3	2.46333333	0.02962731	0.00263333	2.083
DIAST	3	1.44500000	0.06370505	0.01217500	7.636
TOROW	3	1.65000000	0.02362908	0.00167500	2.480
PALW	3	0.90333333	0.00881917	0.00023333	1.691
ROSW	3	1.19333333	0.03609401	0.00390833	5.239
MOL3	3	0.40000000	0.01527525	0.00070000	6.614
PREM	3	0.31833333	0.01481366	0.00065833	8.060
POPAL	3	2.35500000	0.06806859	0.01390000	5.006
BULL	3	1.20000000	0.00763763	0.00017500	1.102
BULW	3	1.12166667	0.01641476	0.00080833	2.535
WIDG	3	4.50833333	0.05833333	0.01020833	2.241
WID2	3	2.78333333	0.02403701	0.00173333	1.496
CONS	3	1.46333333	0.07980880	0.01910833	9.446
DEPT	3	1.95666667	0.02204793	0.00145833	1.952

------------------------ LOCATION=LING SEX=FEMALE ------------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	6.13833333	0.04475241	0.00600833	1.263
BASL	3	5.58000000	0.08504901	0.02170000	2.640
ROSL	3	2.58500000	0.02020726	0.00122500	1.354
NASL	3	2.31500000	0.02309401	0.00160000	1.728
DIAST	3	1.42166667	0.05918427	0.01050833	7.211
TOROW	3	1.62500000	0.02020726	0.00122500	2.154
PALW	3	0.86166667	0.00600925	0.00010833	1.208
ROSW	3	1.10000000	0.01802776	0.00097500	2.839
MOL3	3	0.40833333	0.02773886	0.00230833	11.766
PREM	3	0.31000000	0.00500000	0.00007500	2.794
POPAL	3	2.18000000	0.04769696	0.00682500	3.790
BULL	3	1.08500000	0.03883727	0.00452500	6.200
BULW	3	1.05666667	0.04176655	0.00523333	6.846
WIDG	3	4.34000000	0.07005950	0.01472500	2.796
WID2	3	2.71000000	0.02645751	0.00210000	1.691
CONS	3	1.36333333	0.03086710	0.00285833	3.922
DEPT	3	1.83833333	0.03609401	0.00390833	3.401

LOCATION=LING SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	2	6.39000000	0.08000000	0.01280000	1.771
BASL	2	5.72250000	0.09750000	0.01901250	2.410
ROSL	2	2.73250000	0.02250000	0.00101250	1.164
NASL	2	2.53000000	0.03500000	0.00245000	1.956
DIAST	2	1.48250000	0.04250000	0.00361250	4.054
TOROW	2	1.60000000	0.03500000	0.00245000	3.094
PALW	2	0.89750000	0.01750000	0.00061250	2.758
ROSW	2	1.13500000	0.05500000	0.00605000	6.853
MOL3	2	0.38250000	0.00250000	0.00001250	0.924
PREM	2	0.30750000	0.00250000	0.00001250	1.150
POPAL	2	2.36750000	0.07750000	0.01201250	4.629
BULL	2	1.13750000	0.04750000	0.00451250	5.906
BULW	2	1.08500000	0.03500000	0.00245000	4.562
WIDG	2	4.39500000	0.03500000	0.00245000	1.126
WID2	2	2.71250000	0.00750000	0.00011250	0.391
CONS	2	1.51750000	0.06750000	0.00911250	6.291
DEPT	2	1.98500000	0.00500000	0.00005000	0.356

----------------------- LOCATION=MILN SEX=FEMALE -----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	14	6.00107143	0.03830609	0.02054299	2.388
BASL	14	5.37071429	0.04303033	0.02592253	2.998
ROSL	14	2.52607143	0.01991175	0.00555069	2.949
NASL	14	2.25142857	0.02311241	0.00747857	3.841
DIAST	14	1.33321429	0.01310992	0.00240618	3.679
TOROW	14	1.63785714	0.01535938	0.00330275	3.509
PALW	14	0.86142857	0.01012869	0.00143626	4.399
ROSW	14	1.09357143	0.00949882	0.00126319	3.250
MOL3	14	0.36571429	0.00737268	0.00076099	7.543
PREM	14	0.30571429	0.00412234	0.00023791	5.045
POPAL	14	2.08821429	0.02339700	0.00766387	4.192
BULL	14	1.10071429	0.00740985	0.00076868	2.519
BULW	14	1.01535714	0.01862340	0.00485563	6.863
WIDG	14	4.26750000	0.03756953	0.01976058	3.294
WID2	14	2.65321429	0.02856267	0.01142157	4.028
CONS	14	1.28250000	0.01774166	0.00440673	5.176
DEPT	14	1.85785714	0.00913444	0.00116813	1.840

LOCATION=MILN SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	14	6.31928571	0.03693199	0.01909560	2.187
BASL	14	5.69214286	0.03564058	0.01778352	2.343
ROSL	14	2.66750000	0.02342131	0.00767981	3.285
NASL	14	2.40607143	0.02659825	0.00990453	4.136
DIAST	14	1.42714286	0.01779550	0.00443352	4.666
TOROW	14	1.65821429	0.01260785	0.00222541	2.845
PALW	14	0.86464286	0.00984027	0.00135563	4.258
ROSW	14	1.13892857	0.00943716	0.00124684	3.100
MOL3	14	0.39107143	0.00524610	0.00038530	5.019
PREM	14	0.31392857	0.00423157	0.00025069	5.044
POPAL	14	2.23892857	0.01826378	0.00466992	3.052
BULL	14	1.14321429	0.01743597	0.00425618	5.707
BULW	14	1.04464286	0.01254075	0.00220179	4.492
WIDG	14	4.46321429	0.03549341	0.01763695	2.976
WID2	14	2.76071429	0.02416096	0.00817253	3.275
CONS	14	1.33607143	0.01114562	0.00173915	3.121
DEPT	14	1.95750000	0.01265291	0.00224135	2.419

----------------------- LOCATION=MULE SEX=FEMALE -----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	5	6.03100000	0.12716525	0.08085500	4.715
BASL	5	5.42400000	0.14903355	0.11105500	6.144
ROSL	5	2.45300000	0.09675484	0.04680750	8.820
NASL	5	2.24200000	0.08212186	0.03372000	8.190
DIAST	5	1.33600000	0.04217227	0.00889250	7.058
TOROW	5	1.61600000	0.01568439	0.00123000	2.170
PALW	5	0.84700000	0.01813836	0.00164500	4.789
ROSW	5	1.07200000	0.03716854	0.00690750	7.753
MOL3	5	0.40100000	0.02315167	0.00268000	12.910
PREM	5	0.29800000	0.00374166	0.00007000	2.808
POPAL	5	2.14800000	0.08907300	0.03967000	9.272
BULL	5	1.09800000	0.03502142	0.00613250	7.132
BULW	5	1.02700000	0.03010814	0.00453250	6.555
WIDG	5	4.21400000	0.14232357	0.10128000	7.552
WID2	5	2.65400000	0.06799632	0.02311750	5.729
CONS	5	1.26600000	0.08227089	0.03384250	14.531
DEPT	5	1.84300000	0.03092733	0.00478250	3.752

LOCATION=MULE SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	2	6.31500000	0.05500000	0.00605000	1.232
BASL	2	5.64750000	0.10250000	0.02101250	2.567
ROSL	2	2.59250000	0.00750000	0.00011250	0.409
NASL	2	2.35000000	0.07500000	0.01125000	4.513
DIAST	2	1.36250000	0.04750000	0.00451250	4.930
TOROW	2	1.68500000	0.04000000	0.00320000	3.357
PALW	2	0.92000000	0.02500000	0.00125000	3.843
ROSW	2	1.16500000	0.00000000	0.00000000	0.000
MOL3	2	0.37250000	0.00250000	0.00001250	0.949
PREM	2	0.32000000	0.00000000	0.00000000	0.000
POPAL	2	2.24000000	0.06500000	0.00845000	4.104
BULL	2	1.14250000	0.01750000	0.00061250	2.166
BULW	2	1.01000000	0.00500000	0.00005000	0.700
WIDG	2	4.45000000	0.05000000	0.00500000	1.589
WID2	2	2.75000000	0.07000000	0.00980000	3.600
CONS	2	1.29500000	0.10500000	0.02205000	11.467
DEPT	2	1.95750000	0.00750000	0.00011250	0.542

------------------------- LOCATION=NAVI SEX=FEMALE -------------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	3	6.36333333	0.05166667	0.00800833	1.406
BASL	3	5.75833333	0.03032234	0.00275833	0.912
ROSL	3	2.67666667	0.05101743	0.00780833	3.301
NASL	3	2.34500000	0.03278719	0.00322500	2.422
DIAST	3	1.44500000	0.02753785	0.00227500	3.301
TOROW	3	1.66166667	0.01964971	0.00115833	2.048
PALW	3	0.88500000	0.01322876	0.00052500	2.589
ROSW	3	1.15666667	0.03086710	0.00285833	4.622
MOL3	3	0.37666667	0.01424001	0.00060833	6.548
PREM	3	0.29666667	0.00440959	0.00005833	2.574
POPAL	3	2.30500000	0.00577350	0.00010000	0.434
BULL	3	1.16666667	0.01964971	0.00115833	2.917
BULW	3	1.09833333	0.01641476	0.00080833	2.589
WIDG	3	4.53666667	0.00881917	0.00023333	0.337
WID2	3	2.76000000	0.06144103	0.01132500	3.856
CONS	3	1.41166667	0.05198825	0.00810833	6.379
DEPT	3	1.91000000	0.02466441	0.00182500	2.237

LOCATION=NAVI SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	6	6.23833333	0.08105211	0.03941667	3.183
BASL	6	5.63416667	0.07779692	0.03631417	3.382
ROSL	6	2.63166667	0.03818086	0.00874667	3.554
NASL	6	2.38416667	0.03300042	0.00653417	3.390
DIAST	6	1.40000000	0.03035896	0.00553000	5.312
TOROW	6	1.68250000	0.01030776	0.00063750	1.501
PALW	6	0.89333333	0.01180866	0.00083667	3.238
ROSW	6	1.11416667	0.02399363	0.00345417	5.275
MOL3	6	0.37750000	0.00403113	0.00009750	2.616
PREM	6	0.32000000	0.00500000	0.00015000	3.827
POPAL	6	2.26333333	0.03295620	0.00651667	3.567
BULL	6	1.12416667	0.01567464	0.00147417	3.415
BULW	6	1.06666667	0.02219860	0.00295667	5.098
WIDG	6	4.45666667	0.05418589	0.01761667	2.978
WID2	6	2.76166667	0.04375436	0.01148667	3.881
CONS	6	1.29333333	0.03453662	0.00715667	6.541
DEPT	6	1.93666667	0.02461932	0.00363667	3.114

------------------------ LOCATION=PORT SEX=FEMALE ------------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	32	5.98015625	0.02628405	0.02210723	2.486
BASL	32	5.35156250	0.02827129	0.02557651	2.988
ROSL	32	2.49937500	0.01918153	0.01177379	4.341
NASL	32	2.23421875	0.01777025	0.01010502	4.499
DIAST	32	1.33953125	0.01712054	0.00937961	7.230
TOROW	32	1.59465625	0.01015640	0.00330088	3.603
PALW	32	0.86515625	0.01030650	0.00339917	6.739
ROSW	32	1.08609375	0.00779893	0.00194635	4.062
MOL3	32	0.38234375	0.00516845	0.00085481	7.647
PREM	32	0.31062500	0.00378179	0.00045766	6.887
POPAL	32	2.11718750	0.01919622	0.01179183	5.129
BULL	32	1.10156250	0.00815499	0.00212813	4.188
BULW	32	0.96859375	0.01119438	0.00401006	6.538
WIDG	32	4.19781250	0.02878586	0.02651603	3.879
WID2	32	2.60468750	0.01633189	0.00853538	3.547
CONS	32	1.30125000	0.01587343	0.00806290	6.901
DEPT	32	1.84578125	0.00949615	0.00288566	2.910

LOCATION=PORT SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	46	6.15260870	0.03177926	0.04645638	3.503
BASL	46	5.51663043	0.03840197	0.06783673	4.721
ROSL	46	2.58163043	0.01593317	0.01167784	4.186
NASL	46	2.30760870	0.01860259	0.01591860	5.468
DIAST	46	1.40782609	0.01437057	0.00949961	6.923
TOROW	46	1.59250000	0.00813496	0.00304417	3.465
PALW	46	0.87739130	0.00713354	0.00234082	5.514
ROSW	46	1.11565217	0.00775626	0.00276734	4.715
MOL3	46	0.39163043	0.00450725	0.00093450	7.806
PREM	46	0.30456522	0.00243180	0.00027203	5.415
POPAL	46	2.16978261	0.02308510	0.02451440	7.216
BULL	46	1.12304348	0.00842339	0.00326386	5.087
BULW	46	1.00250000	0.00833877	0.00319861	5.642
WIDG	46	4.36847826	0.03149031	0.04561541	4.889
WID2	46	2.69217391	0.01294139	0.00770406	3.260
CONS	46	1.35597826	0.01342506	0.00829069	6.715
DEPT	46	1.88880435	0.00774937	0.00276243	2.783

---------------------- LOCATION=POR3 SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	4	6.03125000	0.08469000	0.02868958	2.808
BASL	4	5.42500000	0.07536025	0.02271667	2.778
ROSL	4	2.49125000	0.05137181	0.01055625	4.124
NASL	4	2.29875000	0.03478356	0.00483958	3.026
DIAST	4	1.30250000	0.05359960	0.01149167	8.230
TOROW	4	1.59500000	0.03259601	0.00425000	4.087
PALW	4	0.88125000	0.03204001	0.00410625	7.271
ROSW	4	1.12750000	0.03230712	0.00417500	5.731
MOL3	4	0.38500000	0.01338532	0.00071667	6.953
PREM	4	0.31250000	0.00661438	0.00017500	4.233
POPAL	4	2.17750000	0.05092887	0.01037500	4.678
BULL	4	1.09000000	0.02179449	0.00190000	3.999
BULW	4	1.02125000	0.02034853	0.00165625	3.985
WIDG	4	4.32500000	0.12979150	0.06738333	6.002
WID2	4	2.58625000	0.02435630	0.00237292	1.884
CONS	4	1.24750000	0.08337915	0.02780833	13.367
DEPT	4	1.83000000	0.00935414	0.00035000	1.022

LOCATION=POR3 SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	5	6.28100000	0.06925316	0.02398000	2.465
BASL	5	5.64700000	0.05330572	0.01420750	2.111
ROSL	5	2.66200000	0.07567364	0.02863250	6.357
NASL	5	2.45000000	0.02607681	0.00340000	2.380
DIAST	5	1.37700000	0.00463681	0.00010750	0.753
TOROW	5	1.66600000	0.02204541	0.00243000	2.959
PALW	5	0.85000000	0.01151086	0.00066250	3.028
ROSW	5	1.13300000	0.00768115	0.00029500	1.516
MOL3	5	0.38000000	0.00353553	0.00006250	2.080
PREM	5	0.30500000	0.00418330	0.00008750	3.067
POPAL	5	2.22100000	0.01691153	0.00143000	1.703
BULL	5	1.13900000	0.02521904	0.00318000	4.951
BULW	5	1.07200000	0.01847972	0.00170750	3.855
WIDG	5	4.47000000	0.03053686	0.00466250	1.528
WID2	5	2.72400000	0.04246763	0.00901750	3.486
CONS	5	1.31800000	0.02913760	0.00424500	4.943
DEPT	5	1.93900000	0.03280244	0.00538000	3.783

---------------------- LOCATION=ROS1 SEX=FEMALE ----------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	2	5.95750000	0.05250000	0.00551250	1.246
BASL	2	5.34000000	0.04500000	0.00405000	1.192
ROSL	2	2.49500000	0.01500000	0.00045000	0.850
NASL	2	2.19000000	0.01000000	0.00020000	0.646
DIAST	2	1.31000000	0.01500000	0.00045000	1.619
TOROW	2	1.63750000	0.00750000	0.00011250	0.648
PALW	2	0.91250000	0.02750000	0.00151250	4.262
ROSW	2	1.44000000	0.39500000	0.31205000	38.793
MOL3	2	0.37750000	0.00750000	0.00011250	2.810
PREM	2	0.31500000	0.00000000	0.00000000	0.000
POPAL	2	2.10000000	0.01500000	0.00045000	1.010
BULL	2	1.10250000	0.06250000	0.00781250	8.017
BULW	2	0.95750000	0.02750000	0.00151250	4.062
WIDG	2	4.14000000	0.06000000	0.00720000	2.050
WID2	2	2.59500000	0.05000000	0.00500000	2.725
CONS	2	1.20250000	0.04750000	0.00451250	5.586
DEPT	2	1.85000000	0.06000000	0.00720000	4.587

LOCATION=ROS1 SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	5	6.15500000	0.05947689	0.01768750	2.161
BASL	5	5.53100000	0.09162969	0.04198000	3.704
ROSL	5	2.59800000	0.05346962	0.01429500	4.602
NASL	5	2.41100000	0.05182663	0.01343000	4.807
DIAST	5	1.42800000	0.05421254	0.01469500	8.489
TOROW	5	1.58900000	0.01[illegible]96246	0.00199250	2.809
PALW	5	0.87000000	0.02355844	0.00277500	6.055
ROSW	5	1.09900000	0.02501999	0.00313000	5.091
MOL3	5	0.37300000	0.00845577	0.00035750	5.069
PREM	5	0.30500000	0.00353553	0.00006250	2.592
POPAL	5	2.14300000	0.04167133	0.00868250	4.348
BULL	5	1.12300000	0.01504992	0.00113250	2.997
BULW	5	0.99800000	0.03565810	0.00635750	7.989
WIDG	5	4.39800000	0.08474373	0.03590750	4.309
WID2	5	2.67200000	0.03367492	0.00567000	2.818
CONS	5	1.26800000	0.03897435	0.00759500	6.873
DEPT	5	1.92100000	0.01819341	0.00165500	2.118

------------------------ LOCATION=ROS2 SEX=FEMALE ------------------------

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	4	6.03500000	0.02318405	0.00215000	0.768
BASL	4	5.45000000	0.01443376	0.00083333	0.530
ROSL	4	2.48125000	0.02786687	0.00310625	2.246
NASL	4	2.26125000	0.01818596	0.00132292	1.608
DIAST	4	1.34875000	0.03171323	0.00402292	4.703
TOROW	4	1.63250000	0.00478714	0.00009167	0.586
PALW	4	0.92375000	0.04417649	0.00780625	9.565
ROSW	4	1.14750000	0.00968246	0.00037500	1.688
MOL3	4	0.40875000	0.00375000	0.00005625	1.835
PREM	4	0.32375000	0.01106327	0.00048958	6.834
POPAL	4	2.14625000	0.02134781	0.00182292	1.989
BULL	4	1.11250000	0.02393568	0.00229167	4.303
BULW	4	1.00750000	0.03682730	0.00542500	7.311
WIDG	4	4.39375000	0.01841365	0.00135625	0.838
WID2	4	2.73125000	0.03928396	0.00617292	2.877
CONS	4	1.34375000	0.04464560	0.00797292	6.645
DEPT	4	1.88375000	0.02045065	0.00167292	2.171

LOCATION=ROS2 SEX=MALE

VARIABLE	N	MEAN	STD ERROR OF MEAN	VARIANCE	C.V.
TLTH	5	6.22900000	0.07722370	0.02981750	2.772
BASL	5	5.57600000	0.08828080	0.03896750	3.540
ROSL	5	2.60000000	0.04701064	0.01105000	4.043
NASL	5	2.37800000	0.04578755	0.01048250	4.305
DIAST	5	1.38600000	0.03075711	0.00473000	4.962
TOROW	5	1.63100000	0.02431049	0.00295500	3.333
PALW	5	0.89500000	0.00851469	0.00036250	2.127
ROSW	5	1.13500000	0.03952847	0.00781250	7.788
MOL3	5	0.38200000	0.01383835	0.00095750	8.100
PREM	5	0.31800000	0.00994987	0.00049500	6.996
POPAL	5	2.16200000	0.06202016	0.01923250	6.414
BULL	5	1.12900000	0.04093898	0.00838000	8.108
BULW	5	1.04100000	0.02834608	0.00401750	6.089
WIDG	5	4.48300000	0.04810405	0.01157000	2.399
WID2	5	2.66000000	0.10551066	0.05566250	8.870
CONS	5	1.32500000	0.04074310	0.00830000	6.876
DEPT	5	1.93700000	0.01240967	0.00077000	1.433

Appendix II. Results of SS-STP (sums of squares simultaneous test procedure) tests for 17 cranial characters of adult male and female black-tailed prairie dogs from 18 localities in New Mexico. Location abbreviations are as in Fig. 1 of the paper on cranial variation. Nonsignificant subsets of localities are indicated by vertical columns of I's.

Greatest Skull Length

MALES

ALAM	I	
LING	I	I
HYW2	I	I
MILN	I	I
CARZ	I	I
BLAK	I	I
CAPU	I	I
MULE	I	I
POR3	I	I
HAYD	I	I
HYWY	I	I
NAVI	I	I
ROS2	I	I
CLAY	I	I
ROS1	I	I
PORT		I
DORA		I
CAUS		I

FEMALES

NAVI	I			
ALAM	I	I		
LING	I	I	I	
CAPU	I	I	I	
HAYD	I	I	I	I
MULE	I	I	I	I
HYW2	I	I	I	I
HYWY	I	I	I	I
ROS2	I	I	I	I
POR3	I	I	I	I
BLAK	I	I	I	I
CARZ		I	I	I
MILN			I	I
CAUS			I	I
PORT				I
ROS1				I
DORA				I
CLAY				I

Appendix II. Continued.

Basalar Length

MALES	FEMALES
ALAM I	NAVI I
LING II	ALAM II
HYW2 II	HYW2 III
CARZ II	HAYD III
MILN II	MULE III
HAYD II	CAPU III
BLAK II	LING III
POR3 II	ROS2 III
NAVI II	POR3 III
MULE II	BLAK III
CAPU II	HYWY III
HYWY II	MILN III
ROS2 II	CARZ II
CLAY II	PORT I
ROS1 II	ROS1 I
PORT I	CAUS I
DORA I	DORA I
CAUS I	CLAY I

Rostral Length

MALES	FEMALES
HYW2 I	NAVI I
ALAM II	ALAM II
LING II	CAPU II
MILN II	HYW2 II
MULE II	MULE II
POR3 II	HAYD II
CARZ II	LING II
CAPU II	CARZ II
NAVI II	CAUS II
HYWY II	HYWY II
HAYD II	MILN II
ROS2 II	PORT II
ROS1 II	ROS1 II
BLAK II	POR3 II
CLAY II	ROS2 II
PORT II	DORA II
CAUS II	BLAK II
DORA I	CLAY I

Nasal Length

MALES	FEMALES
HYW2 I	LING I
ALAM I	ALAM II
LING II	MULE III
POR3 II	NAVI III
MULE II	CAPU III
CARZ II	HYW2 III
ROS1 II	POR3 III
MILN II	HAYD III
NAVI II	ROS2 III
DORA II	DORA III
ROS2 II	MILN III
CAUS II	BLAK III
CAPU II	CARZ II
CLAY II	CAUS II
BLAK II	PORT I
HYWY II	HYWY I
HAYD II	CLAY I
PORT I	ROS1 I

Diastemal Length

MALES	FEMALES
ALAM I	ALAM I
HYW2 II	LING II
CARZ II	NAVI II
LING II	HYW2 II
DORA II	MULE II
ROS1 II	HAYD II
MILN II	CAUS II
PORT I	CAPU II
CAPU I	HYWY II
MULE I	CARZ II
NAVI I	ROS2 II
HAYD I	PORT I
CLAY I	BLAK I
ROS2 I	MILN I
POR3 I	DORA I
HYWY I	ROS1 I
BLAK I	POR3 I
CAUS I	CLAY I

Appendix II. Continued.

Maxillary Toothrow Length

MALES		FEMALES	
BLAK	I	NAVI	I
NAVI	II	DORA	I
HAYD	III	HAYD	I
POR3	IIII	MILN	I
MILN	IIII	MULE	I
LING	IIIII	ROS1	II
MULE	IIIII	ROS2	II
ROS2	IIIII	HYW2	II
HYWY	IIIII	BLAK	II
CAPU	IIIII	HYWY	II
CARZ	IIIII	POR3	II
CAUS	IIII	PORT	II
DORA	III	CARZ	II
CLAY	II	CAPU	II
HYW2	II	CAUS	II
ALAM	II	CLAY	II
PORT	I	ALAM	II
ROS1	I	LING	I

Palatine Width

MALES		FEMALES
BLAK	I	NO SIGNIFICANT DIFFERENCES
CLAY	I	
ALAM	I	
LING	II	
CARZ	II	
HYW2	II	
HAYD	II	
ROS2	II	
NAVI	II	
MULE	II	
DORA	II	
CAUS	II	
PORT	II	
CAPU	II	
ROS1	II	
MILN	II	
POR3	II	
HYWY	I	

Appendix II. Continued.

Rostral Width

MALES		FEMALES	
ALAM	I	ROS1	I
LING	II	CAUS	II
BLAK	II	LING	II
HYWY	II	ALAM	II
MILN	II	NAVI	II
HYW2	II	ROS2	II
ROS2	II	HYWY	II
POR3	II	POR3	II
CAPU	II	CAPU	II
HAYD	II	HAYD	II
CARZ	II	CARZ	II
CLAY	II	HYW2	II
PORT	I	DORA	II
MULE	I	MILN	I
NAVI	I	MULE	I
ROS1	I	PORT	I
DORA	I	CLAY	I
CAUS	I	BLAK	I

Third Molar Width

MALES		FEMALES	
ALAM	I	ALAM	I
CARZ	II	LING	II
LING	II	ROS2	II
DORA	II	HYW2	II
HYWY	I	BLAK	II
MULE	I	CAPU	II
PORT	I	CAUS	II
MILN	I	POR3	II
CAUS	I	HAYD	I
CAPU	I	PORT	I
HYW2	I	CLAY	I
HAYD	I	ROS1	I
ROS2	I	NAVI	I
CLAY	I	MULE	I
POR3	I	CARZ	I
NAVI	I	MILN	I
ROS1	I	HYWY	I
BLAK	I	DORA	I

Appendix II. Continued.

First Premolar Width

MALES	FEMALES
CLAY I	NO SIGNIFICANT DIFFERENCES
ALAM II	
HAYD II	
HYWY II	
NAVI II	
BLAK II	
LING II	
CAPU II	
MULE II	
ROS2 II	
MILN II	
DORA II	
CARZ II	
HYW2 II	
ROS1 II	
POR3 II	
PORT I	
CAUS I	

Postpalatal Length

MALES	FEMALES
HYW2 I	LING I
LING II	NAVI II
ALAM II	ALAM III
HAYD II	HAYD III
NAVI II	HYW2 III
CARZ II	POR3 III
BLAK II	CAPU III
MILN II	MULE III
HYWY II	BLAK III
CAPU II	ROS2 III
CAUS II	CAUS III
POR3 II	PORT II
MULE II	CARZ II
CLAY II	ROS1 II
DORA II	DORA II
PORT II	MILN I
ROS2 II	CLAY I
ROS1 II	HYWY I

Appendix II. Continued.

Auditory Bulla Length

MALES	FEMALES
NO SIGNIFICANT DIFFERENCES	NAVI I
	HYWY II
	ALAM III
	CARZ III
	CAUS III
	HAYD III
	LING III
	ROS2 III
	ROS1 III
	PORT III
	MILN III
	BLAK III
	POR3 III
	MULE III
	HYW2 III
	DORA III
	CAPU II
	CLAY I

Auditory Bulla Width

MALES	FEMALES
LING I	NAVI I
ALAM II	ALAM I
HYW2 II	LING II
HAYD II	HYW2 III
POR3 III	HYWY III
NAVI III	HAYD III
DORA III	BLAK III
HYWY III	POR3 III
MILN III	CAPU III
ROS2 III	MILN III
CARZ III	MULE III
MULE III	ROS2 III
CAPU II	CARZ III
BLAK II	CAUS III
PORT I	PORT II
ROS1 I	ROS1 II
CLAY I	DORA I
CAUS I	CLAY I

Appendix II. Continued.

Greatest Skull Width

MALES	FEMALES
ALAM I	NO SIGNIFICANT DIFFERENCES
LING II	
HAYD II	
CAPU II	
ROS2 II	
POR3 II	
MILN II	
CARZ II	
NAVI II	
BLAK II	
MULE II	
HYWY II	
ROS1 II	
HYW2 II	
PORT I	
DORA I	
CAUS I	
CLAY I	

Mastoid Breadth

MALES	FEMALES
ALAM I	NAVI I
LING II	ALAM II
HAYD II	ROS2 III
NAVI II	HAYD IIII
MILN II	HYW2 IIII
BLAK II	MULE IIII
CAPU II	CAPU IIII
POR3 II	HYWY IIII
MULE II	BLAK IIII
HYW2 II	MILN IIII
HYWY II	PORT IIII
PORT II	DORA IIII
CARZ II	ROS1 IIII
DORA II	POR3 IIII
ROS1 I	CARZ III
ROS2 I	CLAY II
CLAY I	CAUS II
CAUS I	LING I

Least Interorbital Width

MALES		FEMALES	
HYW2	I	NAVI	I
LING	II	HYWY	II
CAUS	II	HYW2	II
ALAM	II	ROS2	III
MULE	II	HAYD	III
PORT	II	PORT	III
MILN	II	MILN	III
ROS2	II	MULE	III
CARZ	II	ALAM	III
POR3	II	CAUS	III
HYWY	II	BLAK	III
HAYD	II	POR3	III
DORA	II	DORA	III
BLAK	II	CAPU	III
NAVI	II	CARZ	III
CAPU	II	ROS1	III
CLAY	II	CLAY	II
ROS1	I	LING	I

Skull Depth

MALES		FEMALES	
HYW2	I	NAVI	I
BLAK	II	LING	II
MILN	II	CAPU	II
LING	II	CLAY	III
POR3	II	CAUS	III
MULE	II	ROS2	III
ROS2	II	HAYD	III
NAVI	III	MULE	III
CAPU	III	MILN	III
HAYD	III	HYWY	III
ALAM	III	ROS1	III
ROS1	III	PORT	III
CARZ	III	BLAK	III
CLAY	III	ALAM	III
HYWY	III	HYW2	III
PORT	III	POR3	III
CAUS	II	CARZ	II
DORA	I	DORA	I