GENIC AND MORPHOMETRIC VARIATION IN KANGAROO RATS, GENUS *DIPODOMYS*, FROM COASTAL CALIFORNIA

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Genic and morphometric variation was examined among populations of *Dipodomys agilis*, *D. elephantinus*, and *D. venustus* from the Pacific coastal ranges of central and southcentral California to ascertain their systematic relationships. Genic data separated *D. agilis* from *D. elephantinus* and *D. venustus* on the basis of six unique alleles, and the two populations of *D. agilis* were separated from one another by three fixed alleles. *D. elephantinus* and *D. venustus* were not separated from each other by any fixed allelic differences, although *D. venustus* had one allele at a polymorphic locus that was not present in *D. elephantinus*. Multivariate analyses of external and cranial characters placed both populations of *D. venustus* close together, the two populations of *D. agilis* were well separated from *D. venustus* and each other, and *D. elephantinus* was placed apart from *D. venustus*. This study indicates that *D. agilis* is not conspecific with *D. elephantinus* or *D. venustus*. Although *D. elephantinus* differs from *D. venustus* in several morphometric characters, none can reliably differentiate between them. *D. elephantinus* is considered to be a subspecies of *D. venustus* because these taxa are nearly identical genetically, karyotypically, and in bacular morphology. In addition, the degrees of differences in external and cranial characters are similar to those observed among populations of other species of *Dipodomys*.

Key words: *Dipodomys*, kangaroo rat, Heteromyidae, genic variation, morphologic variation, geographic variation, California

The agile kangaroo rat (*Dipodomys agilis*) occupies habitats ranging from pine forests to chaparral-covered slopes in southern California to the sparsely vegetated desert of the Magdalena Plain in southern Baja California (Best, 1983*a*). The elephant-eared kangaroo rat (*D. elephantinus*), which has one of the smallest geographic ranges of any species of *Dipodomys*, occurs on chaparral-covered slopes in Monterey and San Benito counties, California (Grinnell, 1922), from the vicinity of Pinnacles National Monument to near Hernandez. The Santa Cruz kangaroo rat (*D. venustus*) occurs in open-chaparral habitat (Hawbecker, 1940) along the Pacific coast southward from near Palo Alto, Santa Clara Co., to near Santa Margarita, San Luis Obispo Co., California. Thus, the habitats occupied are similar among these species, and their geographic ranges form a non-overlapping, nearly continuous, band along the Pacific coast from central California to southern Baja California.

The taxonomic relationships among *D. agilis, D. elephantinus,* and *D. venustus* have been questioned by several authors (Best, 1992). Grinnell (1922) pointed out that in some morphologic respects, *D. venustus* approached *D. elephantinus,* suggesting that *D. elephantinus* had only recently evolved from *D. venustus.* He speculated that intergradation may occur to the north along the Gabilan Range whereby *D. elephantinus* would merge geographically with *D. venustus.* Grinnell (1922) pointed out that the flaring nasals of *D. elephantinus* distinguished it from *D. venustus* and all other *Dipodomys,* but Best (1986) reported that some specimens of *D. venustus* also have flaring nasals. Hall (1981) indicated that *D. elephantinus* is closely related to and possibly only subspecifically distinct from *D. venustus,* and Williams et al. (1993) remarked that samples of populations of *D. venustus* from the Diablo Range were virtually indistinguishable from *D. elephantinus.* Analyses of karyotypic (Stock, 1974), bacular (Best and Schnell, 1974), and skeletal features (Schnell et al., 1978) indicate a close relationship (possibly conspecific) between *D. elephantinus* and *D. venustus.* This close relationship also is supported by the similarity in their parasitic and phoretic arthropod faunas (Thomas et al., 1991). Comments in Honacki et al. (1982) and Wilson and Reeder (1993) indicated a questionable relationship between *D. elephantinus* and *D. venustus* and further suggested they may be conspecific with *D. agilis.* Hall (1981) pointed out the resemblance in width of the maxillary processes of the zygomatic arches of the skull between *D. agilis* and *D. venustus* and speculated they eventually may be determined to be only subspecifically distinct.

Considering the habitats occupied, morphologic similarities, and nearly contiguous ranges of *D. agilis, D. elephantinus,* and *D. venustus,* it is possible that two or all of these taxa are conspecific. To determine their systematic relationships, we examined genic and morphometric variation among these taxa. Our objectives were to investigate the amount of genic variation, the amount and pattern of interpopulation morphometric variation, and phenetic relationships among populations of *D. agilis, D. elephantinus,* and *D. venustus* and to use these data to determine their taxonomic relationships.

MATERIALS AND METHODS

Genic variation in 39 individuals representing a total of six populations of four species of kangaroo rats was assayed; *D. agilis, D. elephantinus, D. heermanni,* and *D. venustus.* Kangaroo rats were trapped, killed, and tissues (heart, kidney, and liver) were removed and stored in liquid nitrogen until returned to the laboratory. Two populations of *D. agilis* were sampled; four specimens were collected in the Angeles National Forest, 6.4 miles W, 4.0 miles N Wrightwood, T4N, R8W, SW ¼ Sec. 20, Los Angeles Co. (referred to hereafter as *agilis*-1) and five animals representing *agilis*-2 were collected on Black Mountain, 5.3 miles N, 8.8 miles E Hemet, T4S, R2E, SE ¼ Sec. 8, 5,000 feet, Riverside Co. (two specimens) and 7.3 miles N, 9.2 miles E Hemet, T4N, R2E, NW ¼ Sec. 4, Riverside Co. (three specimens). Twelve *D. venustus* were analyzed; 11 were from 1.3 miles E Felton, Santa Cruz Co. (*venustus*-1) and one was from the Hastings Natural History Reservation, 14 miles SE Carmel Valley, Monterey Co. (*venustus*-2). The 14 *D. elephantinus* were collected 1 mile N Pinnacles, San Benito Co. Four *D. heermanni* from 1 mile N Pinnacles, San Benito Co., were used as an outgroup taxon to determine primitive and derived genetic attributes of the ingroup taxa (Baverstock et al., 1979).

Standard starch-gel electrophoresis (Harris and Hopkinson, 1976; Selander et al., 1971) was performed on tissue homogenate; abbreviations and Enzyme Commission numbers (Harris and Hopkinson, 1976), when available, are: aconitase-1,2 (ACON-1,2—4.2.1.3); adenylate kinase-1,2 (AK-1,2—2.7.4.7); albumin (ALB); catalase (CAT—1.11.1.6); creatine kinase-2,3,4 (CK-2,3,4—2.7.3.2); esterase-1,2 (ES-1,2—3.1.1.1); glucose-6-phosphate dehydrogenase-1,2 (GD-1,2—1.1.1.49); glutamate oxalacetate transaminase-1,2 (GOT-1,2—2.6.1.1); hemoglobin (HEM); hexokinase-1,2 (HK-1,2—2.7.1.1); isocitrate dehydrogenase-1,2 (ICD-1,2—1.1.1.42); malate dehydrogenase-1,2 (MDH-1,2—1.1.1.37); purine nucleoside phosphorylase

(NP—2.4.2.1); peptidase B-1,2 (PEPB-1,2—3.4.11); phosphoglucomutase-1,2,3 (PGM-1,2,3—2.7.5.1); 6-phosphogluconate dehydrogenase (PGD—1.1.1.44); sorbital dehydrogenase (SORDH—1.1.1.14); superoxide dismutase (SOD—1.15.1.1); xanthine dehydrogenase-1,2 (XDH-1,2). Loci were designated numerically with "1" representing the most anodally migrating isozyme of a given enzyme.

The method of outgroup comparison (Watrous and Wheeler, 1981) was used to determine primitive and derived character states. In the highly variable ES-2 locus, primitive character states could not be determined as no ingroup taxa shared the same allele with *D. heermanni.* Therefore, data were analyzed by phenetic methods using matrices of genetic similarity (Rogers, 1972). Relationships among taxa were determined by the methods of Fitch and Margoliash (1967) and the unweighted pair-group method using arithmetic averages (UPGMA—Sneath and Sokal, 1973).

For morphometric analyses, specimens were aged according to the cranial criteria of Best and Schnell (1974). We analyzed six external and 14 cranial measurements of 451 adult kangaroo rats. Except for body mass, characters used and methods of measuring follow Best (1978, 1983*a,* 1993). A listing of specimens examined is presented in Appendix I. Eight bacula of *D. venustus* from Santa Cruz Co. were compared to 12 of *D. elephantinus* from San Benito Co. with a one-way analysis of variance. The three bacular characters analyzed were the same as described by Best and Schnell (1974).

Character heterogeneity (between sexes and among the six populations) was tested with a one-way analysis of variance, and a sums-of-squares simultaneous test procedure was used to determine maximally nonsignificant subsets (SS-STP—Gabriel and Sokal, 1969). The average measurements of each character for each population were used in multivariate procedures. These characters were standardized (so that each had a mean of 0 and a standard deviation of 1 across populations), and correlation and distance matrices were calculated. Principal components were calculated from a correlation matrix among characters, and projections of populations were plotted on the first three components. A shortest simply-connected network was computed from a matrix of distances among populations.

Canonical discriminant analysis (considering all characters) was used to characterize populations and to reclassify specimens to give an estimate of the accuracy of the original separation of populations. Morphometric analyses were performed using the programs UNIVAR (D. M. Power, in litt.), SPSS-X (SPSS, Inc., 1983), and NT-SYS (Rohlf et al., 1974).

RESULTS

Genic variation.—Of the 33 presumed loci examined, 10 showed intraspecific or interspecific variation: ACON-1,2; CAT; CK-3; ES-1,2; GD-1; GOT-1; HK-1; PGM-1. Loci that showed no variation within species, among species, or in the outgroup taxon included: AK-1,2; ALB; CK-2,4; GD-2; GOT-2; HEM; HK-2; ICD-1,2; MDH-1,2; NP; PEPB-1,2; PGM-2,3; PGD; SORDH; SOD; XDH-1,2. Allelic frequencies for the variable loci are presented in Table 1. The two populations of *D. agilis* were distinguished from *D. elephantinus* and *D. venustus* by the presence of two unique alleles; GD-1 (95) and PGM-1 (110). *D. elephantinus* and *D. venustus* were not separated by any fixed allelic differences; however, *D. venustus* had two alleles, ES-2 (−50) and CAT (80), that were not present in *D. elephantinus. D. elephantinus* and *D. venustus* both had four alleles not present in *D. agilis*; ACON-1 (105), ES-2 (−100), GD-1 (110), and PGM-1 (100). The outgroup taxon for this study, *D. heermanni,* was similar to the ingroup taxa, *D. elephantinus* and *D. venustus,* and differed by the possession of two unique alleles; ES-2 (200) and GOT-1 (110). In addition, GD-1 (100) and HK-1 (100) were present in all taxa except *D. heermanni.*

A phenogram derived from the genic characteristics of individual animals within the ingroup taxa is presented as Fig. 1. Individuals of *D. elephantinus* and *D. venustus* did not segregate as distinct clusters within the phenogram. However, individuals of *D. elephantinus* and *D. venustus* were separated from those of *D. agilis.* Within *D. agilis,* there were two distinct clusters. *D. agilis* from Los Angeles Co. (*agilis*-1)

TABLE 1.—*Allele frequencies of variable loci for both ingroup and outgroup taxa. Locus abbreviations follow those presented in the text. The common allele is listed as 100.*

	Taxon				
Locus	*agilis-* 1	*agilis-* 2	*ele-phan-tinus*	*ven-ustus*	*heer-manni*
ACON-1					
95	1.000	0.0	0.0	0.0	
100	0.0	1.000	0.786	0.666	
105	0.0	0.0	0.214	0.333	
ACON-2					
100	0.0	1.000	1.000	1.000	
105	1.000	0.0	0.0	0.0	
CAT					
80	0.0	0.0	0.0	0.166	0.0
90	0.250	0.666	0.0	0.083	0.0
100	0.750	0.333	1.000	0.750	1.000
CK-3					
100	0.500	0.0	1.000	1.000	1.000
105	0.0	1.000	0.0	0.0	0.0
110	0.500	0.0	0.0	0.0	0.0
ES-1					
95	0.500	0.0	0.0	0.083	0.500
100	0.0	0.333	0.929	0.917	0.500
105	0.500	0.666	0.071	0.0	0.0
ES-2					
−100	0.0	0.0	0.929	0.666	0.0
−50	0.0	0.0	0.0	0.333	0.0
100	1.000	1.000	0.071	0.0	0.0
200	0.0	0.0	0.0	0.0	1.000
GD-1					
95	0.500	0.500	0.0	0.0	1.000
100	0.500	0.500	0.929	0.917	0.0
110	0.0	0.0	0.071	0.083	0.0
GOT-1					
100	1.000	1.000	1.000	1.000	0.125
110	0.0	0.0	0.0	0.0	0.875
HK-1					
95	0.750	0.0	0.0	0.0	1.000
100	0.250	1.000	1.000	1.000	0.0
PGM-1					
100	0.0	0.0	1.000	0.917	
105	0.0	0.166	0.0	0.0	
110	1.000	0.833	0.0	0.083	

clearly were distinguishable from the rest (*agilis*-2). *Agilis*-1 differed from *agilis*-2 by the possession of three unique alleles; ACON-1 (95), ACON-2 (105), and HK-1 (95). A phenogram representing phenetic relationships among the two populations of *D. agilis, D. elephantinus,* and *D. venustus* is presented as Fig. 2a (*D. heermanni* was not included because data for ACON-1, ACON-2, and PGM-1 were unscorable for that taxon). *D. elephantinus* and *D. venustus* were closer to each other than were the two populations of *D. agilis.*

A Fitch-Margoliash tree representing the postulated phylogenetic relationships among the ingroup and outgroup taxa was generated from a matrix of Rogers (1972) genetic-similarity values between each pair of taxa (Fig. 2b). The tree was drawn to scale and indicates the close relationship between *D. elephantinus* and *D. venustus.* These two taxa appeared to be more closely related to each other than were the two populations of *D. agilis.*

Morphometric variation.—There was significant secondary sexual dimorphism in size in each of the taxa examined. For most characters, males were larger than females; characters exhibiting sexual dimorphism differed among taxa.

Significant interpopulation character variation was detected in all characters when the five populations were examined ($P \leq 0.001$; Table 2). *D. elephantinus* was largest in 17 of 20 characters for males and 18 of 20 characters for females, i.e., all characters except length of body, interorbital width, and width of maxillary arch for males, and interorbital width and length of basioccipital for females. *D. elephantinus* was significantly larger than the others in five and nine characters for males and females, respectively. These characters were basal length, greatest length of cranium, greatest width of cranium, and nasal width for both sexes, and in intermaxillary width for males, and body mass, spread of maxillary arch, lacrimal length, greatest depth of cranium, and zygomatic width for females. The two popu-

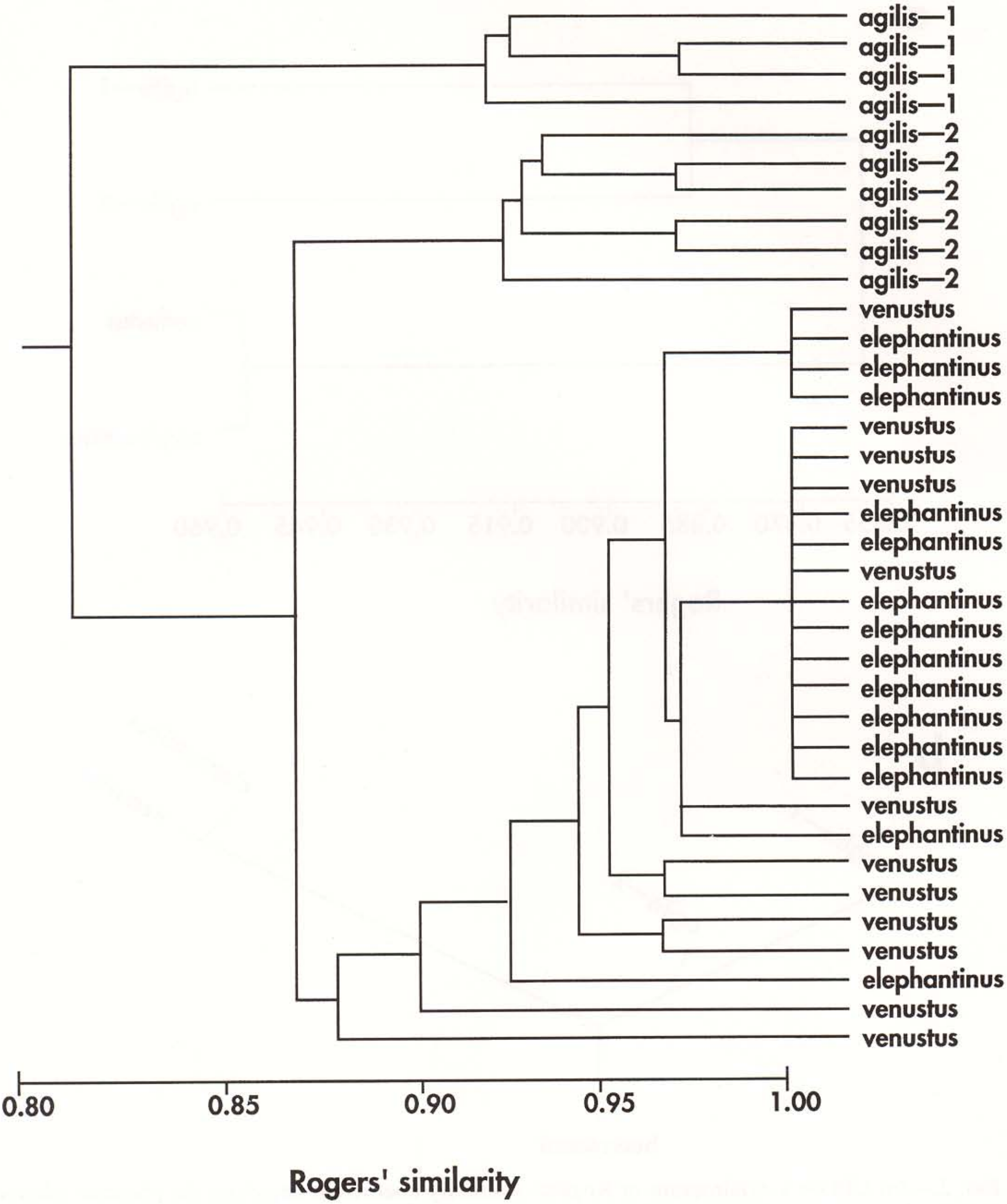

FIG. 1.—Phenogram derived from Rogers' similarity values of genic characteristics of individual specimens of *Dipodomys agilis, D. elephantinus,* and *D. venustus.*

lations of *D. venustus* had means similar to *D. elephantinus* in most characters. *Agilis*-1 was the second smallest in 16 of 20 characters for both sexes. *Agilis*-2 was the smallest in 19 of 20 characters for both sexes. This sample was significantly smaller than the four other populations in length of hind foot, basal length, nasal length, and zygomatic width for both sexes, and in total length, length of tail, greatest length of cranium, spread of maxillary arch, and lacrimal length for males.

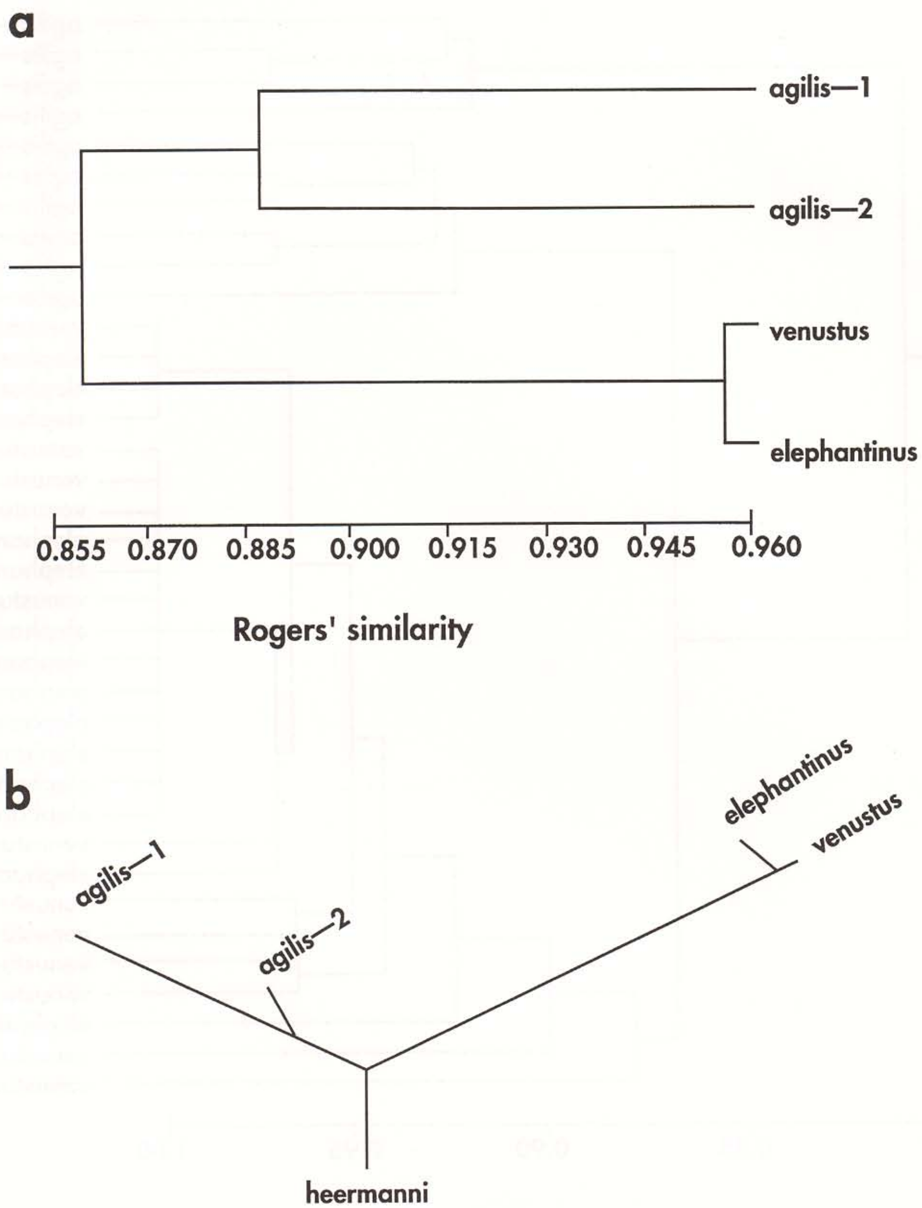

FIG. 2.—(a) UPGMA dendrogram of Rogers' similarity coefficient depicting the phenetic relationship of the *Dipodomys* ingroup taxa based on genic complements. (b) Fitch-Margoliash tree depicting the phenetic relationship between the *Dipodomys* ingroup taxa and the outgroup taxon, *D. heermanni.*

The systematic status of *D. elephantinus* relative to *D. venustus* was evaluated by comparing morphometric variation between these taxa with that between the two populations of *D. agilis.* Data for the populations of *D. venustus* were grouped, and analysis of variance was performed between *D. elephantinus* and *D. venustus* and between *agilis*-1 and *agilis*-2. Means of *D. elephantinus* and *D. venustus* significantly differed in 12 characters for males and 15 characters for females. Means showing no differences were for length of body, length of tail, length of ear, interorbital width, alveolar length, lacrimal length, width of maxillary arch, and basioccipital length for males, and length of tail, interorbital width, nasal length, width of maxillary arch, and basioccipital length for females. For *D. agilis,* means of *agilis*-1 differed from *agilis*-2 in 14 characters for males and 12 for females. Means showing no differences were for length of body, interorbital width, intermaxillary width, alveolar length, greatest depth of cranium, and greatest width of cranium for males, and length of body, length of tail, interorbital width, intermaxillary width, alveolar length, width of maxillary arch, basioccipital length, and greatest depth of cranium for females. Morphologic differences between *D. elephantinus* and *D. venustus* appeared as great as that between the two forms of *D. agilis.* However, a separate study has shown that the two forms of *D. agilis* should be elevated to species-level status (*agilis*-1 = *D. agilis* and *agilis*-2 = *D. simulans*—R. M. Sullivan and T. L. Best, in litt.). Thus, this comparison of morphometric differences implies species-level designations for *D. agilis, D. elephantinus, D. simulans,* and *D. venustus.*

Results of analyses of three bacular characters indicated no significant differences between *D. elephantinus* and *D. venustus* ($P \leq 0.05$). Means and standard deviations for the three bacular characters for *D. elephantinus* and *D. venustus,* respectively, were: length 11.20 ± 0.64, 11.24 ± 0.32; width of base, 2.40 ± 0.20, 2.48 ± 0.31; height of base, 2.49 ± 0.17, 2.41 ± 0.21.

Three-dimensional projections of the five populations of *Dipodomys* on the first three axes derived from principal-components analyses of 20 morphometric characters are depicted in Fig. 3. The three components explained ca. 100% of the total character variation for each gender. Thus, distortion of phenetic distances among populations was relatively small when the character space was reduced to three dimensions.

The character correlations with principal-component I for both sexes were high (>0.7) and positive for all characters. Following the reasoning of previous authors (Baumgardner and Kennedy, 1993; Best, 1978, 1983*a,* 1983*b,* 1993; Johnston and Selander, 1971; Kennedy and Schnell, 1978; Niles, 1973), this component may be taken to represent overall size in both sexes because it accounts for most of the covariation among characters. For both sexes, Population 3 (*D. elephantinus*) had the highest loading along component I and Population 2 (*agilis*-2) had the least values (Fig. 3). This component accounted for ca. 88% of the phenetic variation. The largest animals are to the right side of Fig. 3.

On principal-component II, length of ear (−0.7) and interorbital width (0.4) had highest loadings for males and interorbital width (−0.5) and lacrimal length (0.6) had highest loadings for females. Other characters for both sexes had weak associations. The 6% of the variance accounted for by this component was shown by relatively little separation of populations (Fig. 3).

The third principal component had low loadings for all characters. Only ca. 3% of the phenetic variance was explained by component III. No particular trends could be detected along this component (Fig. 3).

When *D. heermanni* was included in a separate principal-components analysis (not depicted) the relative position of the other five populations was unchanged. *D. heermanni* was placed nearest to *agilis*-1 and was well separated from all populations by its high negative loading on component II for both sexes.

Discriminant analyses, conducted for each sex, were used to assess separation of individuals based on 20 morphometric characters. Analyses of the five populations (i.e., *agilis*-1, *agilis*-2, *elephantinus, venustus*-1, *venustus*-2) correctly classified 88% of males and 85% of females (Table 3). Only one specimen of *agilis*-1 was classified as *agilis*-2 and only three *agilis*-2 were classified as *agilis*-1. Four specimens of *D. agilis* were classified as *D. elephantinus* or *D. venustus.* Seven specimens of *D. elephantinus* were classified as *D. ven-*

TABLE 2.—*Variation in means of 20 external and cranial characters of five populations of kangaroo rats. Statistically homogeneous subsets derived from SS-STP analyses are shown by lines below the sample number and ranked means (1 =* agilis-*1, 2 =* agilis-*2, 3 =* elephantinus, *4 =* venustus-*1, 5 =* venustus-*2).*

Character	Males					Females				
	Results of SS-STP					Results of SS-STP				
External										
Total length	3	4	5	1	2	3	4	5	1	2
	326.2	319.7	313.4	305.7	289.4	322.5	314.4	310.3	293.6	285.8
Length of body	4	3	5	1	2	3	5	4	1	2
	130.4	129.0	123.6	119.8	116.8	128.9	123.6	122.7	117.3	114.3
Length of tail	3	4	5	1	2	3	4	5	1	2
	196.7	193.9	189.7	185.9	172.3	192.6	191.8	186.7	176.5	171.6
Length of hind foot	3	4	5	1	2	3	5	4	1	2
	46.7	46.0	45.1	45.0	41.8	46.8	45.6	45.0	43.2	41.7
Length of ear	3	4	1	5	2	3	4	1	5	2
	19.2	19.0	18.6	17.1	16.6	19.5	18.6	17.8	16.8	16.4
Body mass	3	5	1	4	2	3	5	1	4	2
	88.2	82.7	77.3	77.1	66.6	83.7	74.8	72.6	70.1	61.3
Cranial										
Basal length	3	4	5	1	2	3	4	5	1	2
	24.2	23.7	23.4	23.0	21.9	24.3	23.3	23.3	22.8	21.9
Greatest length	3	4	5	1	2	3	4	5	1	2
	42.6	41.8	41.3	40.4	39.4	42.5	41.1	40.9	39.8	39.2
Spread of maxillary arch	3	5	4	1	2	3	5	4	1	2
	22.8	22.5	22.0	21.5	20.7	22.8	21.7	21.7	21.0	20.6
Interorbital width	5	4	3	1	2	4	5	3	1	2
	11.2	11.0	11.0	10.8	10.6	11.0	11.0	11.0	10.5	10.5
Nasal length	3	4	5	1	2	3	4	5	1	2
	15.7	15.7	15.2	14.9	14.4	15.6	15.4	15.4	14.8	14.1
Intermaxillary width	3	4	5	1	2	3	4	5	1	2
	7.9	7.7	7.6	7.5	7.4	7.8	7.6	7.5	7.4	7.3
Alveolar length	3	4	5	1	2	3	4	5	1	2
	5.4	5.3	5.3	5.0	4.9	5.5	5.3	5.2	5.0	4.9
Lacrimal length	3	1	5	4	2	3	1	4	5	2
	3.9	3.8	3.8	3.8	3.6	4.1	3.8	3.7	3.6	3.4
Width of maxillary arch	4	5	3	1	2	3	4	5	1	2
	5.3	5.3	5.2	5.0	4.8	5.2	5.2	5.1	4.9	4.9
Length of basioccipital	3	4	5	1	2	4	3	5	1	2
	6.1	6.1	6.0	5.8	5.6	6.0	6.0	5.8	5.6	5.6
Greatest depth	3	5	4	1	2	3	5	4	1	2
	14.0	13.8	13.7	13.4	13.3	14.0	13.6	13.5	13.2	13.2

TABLE 2.—*Continued.*

Character	Males					Females				
	Results of SS-STP					Results of SS-STP				
External										
Greatest width	3	5	4	2	1	3	5	4	2	1
	25.9	25.4	25.0	24.5	24.4	25.9	24.9	24.6	24.4	24.0
Zygomatic width	3	5	4	1	2	3	5	4	1	2
	21.0	20.6	20.5	19.7	18.8	21.0	20.1	19.9	19.4	18.8
Nasal width	3	4	5	1	2	3	4	5	1	2
	4.5	4.3	4.2	4.0	3.9	4.6	4.2	4.1	3.9	3.8

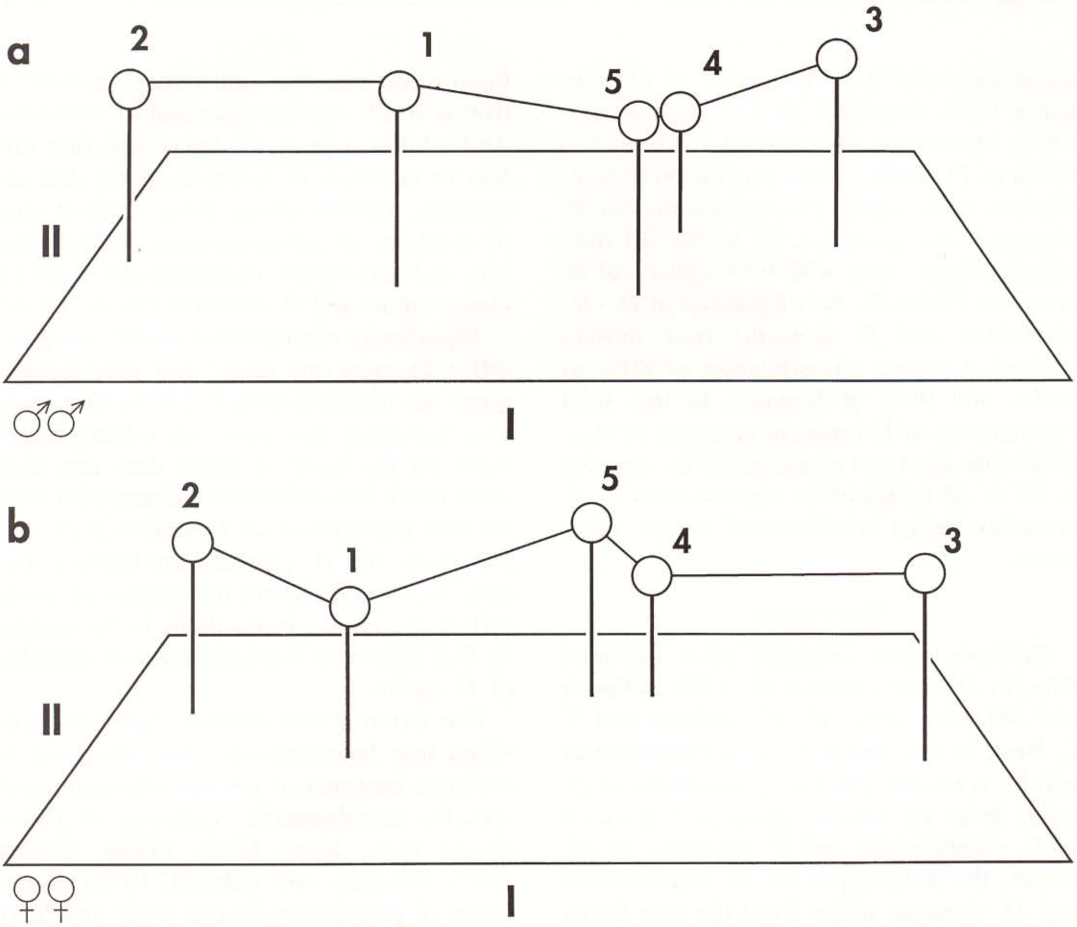

FIG. 3.—Three-dimensional projections of populations (1, *Dipodomys agilis*-1; 2, *D. agilis*-2; 3, *D. elephantinus*; 4, *D. venustus*-1; 5, *D. venustus*-2) onto the first three principal-component axes of variation in the matrix of correlations of 20 morphologic characters for males (a) and females (b). The shortest simply-connected networks, derived from the matrix of distance coefficients for the same characters are superimposed on the plots.

TABLE 3.—*Discriminant analyses among five populations of California kangaroo rats (*Dipodomys*). Based on 20 morphological characters, 88.1% of the grouped cases for males and 85.3% for females were correctly classified.*

Actual group	*n* cases	Gender	Predicted group membership (%) 1	2	3	4	5
1 *agilis*-1	27	♂♂	24 (88.9)	0 (0)	0 (0)	2 (7.4)	1 (3.7)
	16	♀♀	14 (87.5)	1 (6.3)	1 (6.3)	0 (0)	0 (0)
2 *agilis*-2	33	♂♂	1 (3.0)	32 (97.0)	0 (0)	0 (0)	0 (0)
	25	♀♀	2 (8.0)	23 (92.0)	0 (0)	0 (0)	0 (0)
3 *elephantinus*	28	♂♂	0 (0)	0 (0)	23 (82.1)	1 (3.6)	4 (14.3)
	24	♀♀	0 (0)	0 (0)	22 (91.7)	0 (0)	2 (8.3)
4 *venustus*-1	24	♂♂	1 (4.2)	0 (0)	1 (4.2)	20 (83.3)	2 (8.3)
	37	♀♀	2 (5.4)	0 (0)	1 (2.7)	29 (78.4)	5 (13.5)
5 *venustus*-2	6	♂♂	0 (0)	0 (0)	0 (0)	1 (16.7)	5 (83.3)
	7	♀♀	0 (0)	0 (0)	0 (0)	2 (28.6)	5 (71.4)

ustus and only two specimens of *D. venustus* were classified as *D. elephantinus*. Three specimens of *venustus*-1 were classified as *D. agilis*. Thus, separation of populations of *D. agilis, D. elephantinus,* or *D. venustus* was accurate; 15 of the 30 misclassifications were within *D. agilis* and *D. venustus* (Table 3). A comparison of *D. elephantinus* and *D. venustus* (not shown) yielded a correct classification of 80% of males and 98% of females. In this final comparison, differences in accuracy of classifications between sexes primarily was due to 13 of 58 males of *D. elephantinus* or *D. venustus* being misclassified as the other taxon.

DISCUSSION

Previous genic analyses have included data for *D. agilis* (Best et al., 1986; Johnson and Selander, 1971; R. M. Sullivan and T. L. Best, in litt.), but not for *D. elephantinus* and *D. venustus*. The two populations of *D. agilis* have six unique alleles not detected in *D. elephantinus* and *D. venustus*. In addition, the karyotypes of *D. elephantinus* and *D. venustus* differ from the two forms of *D. agilis* (Stock, 1974). Although *agilis*-2, *D. elephantinus,* and *D. venustus* have karyotypes with 2n = 60, *agilis*-2 has 23 submetacentric autosomes, instead of 21 as in *D. elephantinus* and *D. venustus,* and three subtelocentric autosomes instead of five as in *D. elephantinus* and *D. venustus*. *Agilis*-1 has a 2n = 62 karyotype that differs in numbers of submetacentric and acrocentric chromosomes from *agilis*-2, and in numbers of submetacentric, subtelocentric, and acrocentric chromosomes from *D. elephantinus* and *D. venustus* (Stock, 1974).

Dipodomys elephantinus and *D. venustus* differ in only one allele and their karyotypes are identical (Stock, 1974). Our analyses indicated they were not reliably separated on the basis of genic data and they were much less differentiated genically than the two populations of *D. agilis*. If *D. elephantinus* and *D. venustus* are distinct species, we would expect the degree of genic differentiation between them to be similar to that observed between the two samples of *D. agilis*.

Our external and cranial characters provided less heterogeneity than observed in previous analyses of interspecific and intraspecific morphometric variation in *Dipodomys* (e.g., Best, 1978, 1983*a*, 1983*b*, 1993; Kennedy and Schnell, 1978). Separation of populations in our study primarily was on the basis of body size. Univariate analyses indicated *D. elephantinus* was significantly larger than other populations in several characters and *agilis*-2 was smaller. The two populations of *D. venustus* were similar and often were undifferentiated from *agilis*-1. The large ear of *D. elephantinus* separates it from most other *Dipodomys* (Best, 1993; Grinnell, 1922), but our analyses indicated there was overlap among populations in length of ear; the average for *D. elephantinus* was the largest and differed significantly from *agilis*-2, the smallest in both sexes.

We detected significant differences in external and cranial characters between the two populations of *D. agilis.* This agrees with the findings of R. M. Sullivan and T. L. Best (in litt.) who examined a larger sample of *D. agilis* from southern California and Baja California. They concluded there were two distinct species that could be separated based upon significant differences in external and cranial characters, bacula, karyotypes, and genic data.

Grinnell (1922) noted that the flaring nasals of *D. elephantinus* distinguished that taxon from all other species of *Dipodomys.* Our data on nasal width substantiates Grinnell's observation, although some *D. venustus* also have flaring nasals (Best, 1986). The degree of difference in external and cranial morphology between *D. elephantinus* and *D. venustus* is similar to that present between the two populations of *D. agilis,* which are considered to be separate species. The morphologic differences between *D. elephantinus* and *D. venustus* could be interpreted to indicate that the two are specifically distinct; however, substantial amounts of morphologic variation have been observed within other species of *Dipodomys* that occupy geographic distributions of similar extent as that of the combined ranges of *D. elephantinus* and *D. venustus.* Best (1987) reported significant differences among samples of *D. elator* for 11 and 9 of 19 morphologic characters in males and females, respectively. Similar results have been reported for *D. gravipes* (12 and 11 of 19 characters for males and females, respectively—Best, 1983*b*) and *D. nitratoides* (16 and 17 of 19 characters for males and females, respectively—G. D. Baumgardner, pers. comm.). The variation we observed between *D. elephantinus* and *D. venustus* is consistent with the intraspecific variation reported in these other species of kangaroo rats.

Comparisons of bacular data for the two forms of *D. agilis* indicated they were different (R. M. Sullivan and T. L. Best, in litt.). Best and Schnell (1974) examined only one baculum of *D. elephantinus* and six of *D. venustus.* Their specimen of *D. elephantinus* probably was a subadult; it was smaller than those subsequently collected from adult specimens and analyzed herein. Best (1986) presented drawings of representative bacula for *D. elephantinus,* and Best and Schnell (1974) depicted bacula of an adult *D. venustus,* which appear similar. Our analyses of new bacular data have shown no differences between *D. elephantinus* and *D. venustus.*

Most of the variation among the five populations studied here was in size differences; this was reflected in the three-dimensional plots. There was a similar degree of separation between the two populations of *D. agilis,* between *D. agilis* and the two populations of *D. venustus,* and between the two populations of *D. venustus* and *D. elephantinus.* Analyses indicated *D. elephantinus* and *agilis*-1 differed in size from *D. venustus* to about the same degree, again showing differences in external and cranial morphology between *D. elephantinus* and *D. venustus.*

Discriminant analyses previously have been performed on populations of *D. agilis.* Best (1983*a*) compared northern, southern, and unknown individuals in an attempt to elucidate breaks in morphologic variation within the range of that species. He presented histograms that indicated much overlap between the three groups of specimens and he was unable to detect clinal discontinuities. However, using chromosomal number as a guide, R. M. Sullivan and T. L. Best (in litt.) separated specimens of the northern and southern forms of *D. agilis.* They detected little overlap in results of discriminant analyses of morphologic attributes between the 2n = 60 and 2n = 62 chromosomal forms and recommended they be considered as two species, *D. agilis* and *D. simulans.* Our discriminant analyses yielded similar results for the populations analyzed and showed some overlap in morphology between *D. elephantinus* and *D. venustus.*

Dipodomys agilis occupies many habitats in southern California and Baja California (Best, 1983*a*). The northern form primarily is a montane species that lives on chaparral-covered slopes upward to coniferous forests. The southern form occupies more diverse habitats from deserts to coniferous forests. Where their ranges approach each other in the Los Angeles Basin, they appear to be ecologically separated (R. M. Sullivan and T. L. Best, in litt.).

Best (1986) pointed out that habitat occupied by *D. elephantinus* near Pinnacles, San Benito Co., is quite different from the open habitat described by Hawbecker (1940) from *D. venustus* near Santa Cruz, Santa Cruz Co. Best (1986) speculated that difference in habitat occupied may be related to the sympatric occurrence of *D. heermanni* with *D. elephantinus* near Pinnacles. Perhaps ecologic pressures from a congener have caused *D. elephantinus* to inhabit only the dense chaparral, with *D. heermanni* being present throughout the area. Possibly because there are no other congeners that occur with *D. venustus* in the vicinity of Santa Cruz, it occupies more open habitat than southern populations. M. Nachman (pers. comm.) found *D. elephantinus* in more open habitat near Hernandez, San Benito Co., an area where it is not sympatric with any other species of *Dipodomys.* Although *D. elephantinus* seems to live under a more dense canopy of vegetation than *D. venustus,* both occupy open habitats when congeners are absent. Thus, the range of habitats occupied does not entirely support species-level differences between these two taxa.

We conclude that *D. agilis* is not conspecific with *D. elephantinus* or *D. venustus,* although it is considered a closely related member of the *heermanni* group of kangaroo rats (Lidicker, 1960; Setzer, 1949). Karyotypic (Stock, 1974), genic, and bacular data indicate *D. elephantinus* and *D. venustus* are conspecific. *D. elephantinus* differs from populations of *D. venustus* in several cranial characters, which led Grinnell (1919, 1921, 1922) to conclude that they were distinct species. Because the morphometric differences observed between *D. elephantinus* and *D. venustus* are similar to those observed within other species of *Dipodomys* and because these two forms have nearly identical karyotypes, bacula, and genic data, we believe they represent one species. *D. elephantinus* and *D. venustus* do not exhibit as much differentiation as between the two groups of *D. agilis* (R. M. Sullivan and T. L. Best, in litt.); i.e., in chromosomal number and configuration, bacular morphology, and cranial morphology. We know of no areas of sympatry of *D. elephantinus* and *D. venustus,* although Grinnell (1922) believed they may intergrade along the Gabilan Range.

According to our findings, the correct names for *D. elephantinus* and *D. venustus* (with synonyms indented) are as follows:

Dipodomys venustus venustus (Merriam, 1904)
  Perodipus venustus Merriam, 1904
Dipodomys venustus elephantinus (Grinnell, 1919)
  Perodipus elephantinus Grinnell, 1919
Dipodomys venustus sanctiluciae Grinnell, 1919
  Dipodomys sanctiluciae Grinnell, 1919

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Appendix I

Specimens included in morphologic analyses. Museum acronyms are given in the acknowledgments.

Population 1.—Dipodomys agilis-1 (36 males, 28 females). *Los Angeles Co.*: 6 miles S, 2 miles E Acton (2, 1 LBSC); Aliso Canyon (1, 0 RGH); Angeles National Forest, South Fork Camp (0, 1 LBSC); Angeles National Forest, South Fork Camp near Valyermo (2, 0 LBSC); 1 mile SE Big Pine, San Gabriel Mountains, 6,600 feet (2, 1 KU); 6 miles W Big Pines Camp, 5,280 feet (1, 0 LBSC); Chalao Flats (1, 0 LACM); Horse Flats Campground, San Gabriel Mountains (1, 1 LACM); Horse Flats, San Gabriel Mountains (2, 2 LACM); Little Gleason, 5,700 feet (1, 0 RGH); Little Rock Public Campground, 3½ miles S, 2½ miles W Little Rock (0, 1 LACM); 3½ miles NW Mill Creek Summit (2, 3 LBSC; 0, 1 UA); 3½ miles NW Mill Creek Summit (0, 1 UA); Mount Gleason, 6,300 feet (0, 1 RGH); 4 miles S Pearblossom, 4,600 feet (0, 1 RGH); 5 miles S Pearblossom, 4,600 feet (0, 1 RGH); 5 miles S, 0.6 mile E Pearblossom (3, 0 RGH); Pleasant View Ridge, Juniper Hills, 4,800 feet (0, 1 KU); N side San Gabriel Mountains, Pleasant View Ridge, Juniper Hills, 4,800 feet (4, 2 UA); Santiago Canyon, Angeles National Forest (1, 2 LACM); ½ mile N South Fork Camp, Angeles National Forest (0, 1 LBSC); South Fork Camp near Valyermo (1, 0 LBSC); 2 miles S South Fork Public Camp, Angeles National Forest, 4,500 feet (1, 0 LACM); Swartout Valley, Big Pine, 6,900 feet (1, 2 UCLA); 5 miles SE Valyermo, San Gabriel Mountains (2, 0 KU); 5 miles SE Valyermo, San Gabriel Mountains, 5,200 feet (1, 0 KU); 10 miles SE Valyermo, San Gabriel Mountains, 5,200 feet (1, 0 KU); 3 miles NE Wrightwood, 3,800 feet (1, 0 LBSC); 3 miles NE Wrightwood on state highway 2, 3,800 feet (1, 0 LBSC); 6.4 miles W, 4.0 miles N Wrightwood, T4N, R8W, SW ¼ Sec. 20, Angeles National Forest (2, 3 MSB); 11.2 miles W, 5.1 miles N Wrightwood, T4N, R9W, SE ¼ Sec. 16 (1, 0 MSB). *San Bernardino Co.*: Cajon Pass (0, 1 USNM); Lytle Creek (0, 1 USNM); Lytle Creek Canyon, Applewhite Campgrounds (1, 0 LBSC).

Population 2.—Dipodomys agilis-2 (48 males, 32 females). *Riverside Co.*: Aguanga (1, 2 SDNHM); ¼ mile ENE Aguanga, 2,050 feet (1, 2 MVZ); 1¼ miles N, 1.3 mile E Aguanga, 2,300 feet (0, 1 MVZ); 4 miles N Aguanga, Wilson Creek, 2,500 feet (7, 2 RGH); 5 miles E, 3 miles N Aguanga (3, 3 RGH); 6 miles E Aguanga (1, 0 RGH); 1 mile S Dripping Springs (1, 0 RGH); Radec, 2,000 feet (0, 2 USNM); 11 miles SE Temecula at Dripping Springs (1, 1 LBSC). *San Diego Co.*: 3 miles SE Aguanga, 2,600 feet (3, 0 MVZ); Banner (1, 0 MVZ; 0, 1 SDNHM); Grapevine Springs (1, 0 MVZ); 10 miles N Julien on county road 52 (1, 0 MVZ); 15 miles N Julien on county road 52 (1, 0 MVZ); Mann Ranch (W side firebreak) ½ mile W Oak Grove, 2,800 feet (2, 0 MVZ); Mann Ranch, ½ mile NW Oak Grove, 2,800 feet (1, 2 MVZ); North Peak, Cuyamaca Mountains (0, 1 SDNHM); Oak Grove (2, 0 SDNHM); 2½ miles N Oak Grove (4, 4 SDNHM); Oak Grove Forest Camp

(3, 2 LBSC); 20 miles S Oak Grove Public Campground, take N fork 2 miles E (1, 0 LBSC); Ranchito Road, 2 miles E San Diego highway 2 (1, 0 LBSC); 2 miles E on San Diego 2 from North Scissors (1, 0 LBSC); 2 miles E San Diego 2 on road to Ranchito (2, 2 LBSC); Santa Ysabel (2, 2 AMNH; 1, 0 FMNH; 0, 2 USNM); Scissors Crossing, Earthquake Valley (0, 1 MVZ); Silverent Palomar Mountain (1, 1 SDNHM); Sourdough Springs, T20S, R1E, Cleveland National Forest, 6,140 feet (2, 0 MSB); 6.7 miles NW Warner Springs, Cleveland National Forest (3, 1 MSB); 1 mile W Warner's Hot Springs (1, 0 SDNHM).

Population 3.—Dipodomys elephantinus (38 males, 32 females). *Monterey Co.*: Priest Valley, 2,500 feet (1, 1 MVZ). *San Benito Co.*: Bear Valley (3, 0 USNM); Butts Ranch, 3,300 feet, 5 miles NNE San Benito (1, 0 MVZ); Cook Post Office, 1,300 feet, Bear Valley (5, 6 MVZ); 1 mile N Cook Post Office, 1,300 feet, Bear Valley (5, 3 MVZ); 1 mile S Cook Post Office=Pinnacles (5, 1 SDNHM); Laguna Ranch, 4,000 feet, 4 miles S Hernandez (7, 9 MVZ); 1 mile N Pinnacles (7, 6 OU); 3¾ miles E, 1 mile S San Benito (1, 0 MVZ); 5 miles ENE San Benito, 3,700 feet (0, 1 MVZ); 1 mile SE San Benito Mountain, 4,400 feet (0, 2 MVZ); Summit San Benito Mountain, 5,250 feet (2, 0 MVZ); 1 mile SE Summit San Benito Mountain, 4,000–4,400 feet (1, 3 MVZ).

Population 4.—Dipodomys venustus-1 (48 males, 57 females). *Monterey Co.*: Fremont Peak, Gabilan Range (1, 3 USNM). *San Benito Co.*: Fremont Peak, 7 miles S San Juan, 2,800 feet (0, 3 MVZ); Fremont Peak Road, 7 miles S San Juan, 2,800 feet (0, 1 MVZ); 4¼ miles S, 4¾ miles E San Juan Batista (1, 0 MVZ). *Santa Clara Co.*: Mount Hamilton (1, 0 CAS); Stanford University (1, 0 MVZ). *Santa Cruz Co.*: Bear Creek, 2 miles NE Boulder Creek, 650 feet (2, 1 MVZ); Ben Lomond (1, 0 CAS); Ben Lomond, 300 feet (1, 1 SDNHM); Berglund Ranch, 2 miles NW Corralitos, 1,250 feet (6, 4 MVZ); 1 mile NE Bonny Doon, 1,700 feet (1, 1 MVZ); 1 mile NNE Bonny Doon (1, 2 MVZ); 2 miles NW Corralitos (4, 7 OU); Doyle Gulch, 9 miles NE Santa Cruz (3, 4 MVZ); Enos Ranch, 1 mile NW Corralitos, 700 feet (0, 3 MVZ); Graham Hill (0, 1 CAS); Graham Hill Road 1.1 miles from Felton Station (0, 1 MVZ); Graham Hill Road, 1.1 miles SE Felton Station (2, 2 MVZ); head of Doyle Gulch (3, 5 MVZ); J. Enos Ranch, 1¼ miles NW Corralitos, 700 feet (0, 1 MVZ); Mount Hermon (0, 1 MVZ); Mount Hermon Road, 1.3 miles E Mount Hermon (0, 1 MVZ); Santa Cruz (5, 2 MVZ; 9, 7 USNM); 5 miles N Santa Cruz (1, 1 MVZ); 6 miles N Santa Cruz, Graham Hill, 800 feet (3, 3 SDNHM); 5 miles N Soquel, in Rodeo Gulch (0, 1 CAS); top Santa Cruz Mountains, near Santa Cruz (1, 0 USNM); Zayante Road, 2.1 miles E Ben Lomond (1, 1 MVZ).

Population 5.—Dipodomys venustus-2 (17 males, 16 females). *Monterey Co.*: 1¼ miles S Chalk Peak, 3,000 feet (1, 1 MVZ); Chews Ridge, Santa Lucia Mountains, 5,000 feet (1, 2 MVZ); Hastings Natural History Reservation, Carmel Valley, 1,800 feet (1, 0 MVZ); Hastings Natural History Reservation, 14 miles SE Carmel Valley (1, 1 MVZ); Hastings Reservation, 2,000 feet (1, 1 MVZ); head of Caves Trail, Santa Lucia Mountains, 4,600 feet (0, 1 MVZ); Jolon (3, 2 AMNH); 2–2½ miles W Jolon, San Antonio River, ca. 2,000 feet (1, 1 MVZ); no precise locality (2, 0 PSM); Santa Lucia Peak (2, 1 USNM); Summit of Santa Lucia Peak, 5,844 feet (1, 1 MVZ). *San Luis Obispo Co.*: DeTracey Ranch, Santa Lucia Mountains, 1,250 feet (1, 0 MVZ); Indian Creek, 13 miles S Shandon, 1,500 feet (0, 1 MVZ); Red Eagle Mine, 15 miles S Shandon (1, 1 PSM); Santa Margarita, 996 feet (1, 3 MVZ).

Population 6.—Dipodomys heermanni (50 males, 50 females). *Fresno Co.*: Coalinga, mouth of Warthon Canyon (4, 2 SDNHM). *Kern Co.*: McKittrick (0, 1 SDNHM). *Modoc Co.*: 3½ miles E Likely (1, 0 LACM). *Monterey Co.*: 2 miles N highway 146, 1.7 miles W Chaparral Ranger Station, Pinnacles National Monument, 1,750 feet (0, 1 LACM): 1 mile SW Jolon (6, 5 SDNHM); King City (0, 1 SDNHM); 7 miles NE Monterey (0, 1 LACM); Pleyto (1, 0 SDNHM); 3 miles W Salinas (0, 1 LACM). *San Benito Co.*: Bear Valley (1, 0 SDNHM); Bear Valley, along road leading to Pinnacles National Monument (0, 2 LACM); 1 mile S Cook Post Office=Pinnacles (0, 6 SDNHM). *San Luis Obispo Co.*: E end Cuyama Valley (2, 1 SDNHM); Gypsum Canyon and Cuyama River Gorge along the Santa Barbara Co. line, ca. 5–6 miles E Pine Canyon Ranger Station (=24 miles E Nipomo) (1, 1 LACM); 2 miles W of highway 166 from Pine Canyon Ranger Station, Cuyama River Gorge (=13 miles E Nipomo) (0, 2 LACM); 8 miles S Morro (20, 12 SDNHM); San Juan Creek (1, 2 SDNHM); 2

miles E San Juan Creek (0, 2 SDNHM); 9 miles E Simmler (1, 0 SDNHM); 10 miles W Simmler (0, 2 SDNHM); 7 miles S Simmler, Carrizo Plain (0, 2 SDNHM). *Santa Barbara Co.*: junction Clear Creek and Cuyama River (=20 miles NE Santa Maria) (1, 0 LACM); junction Cuyama River and Sisquoc River (=1 mile N Garey) (2, 0 LACM); 2 miles NNW Lompoc (6, 3 LACM); 8 miles S Santa Maria Station (1, 0 SDNHM); Sierra Madre Picnic Area off highway 166, Cuyama Valley Gorge (=19 miles NE Santa Maria) (0, 1 LACM); Vandenburg Air Force Base (1, 0 SDNHM); Vandenburg Air Force Base, dunes near mouth San Antonio (0, 1 SDNHM); Vandenburg Air Force Base, Sudden Ranch Area (1, 1 SDNHM).