# SYSTEMATICS AND MORPHOLOGIC VARIATION IN TWO CHROMOSOMAL FORMS OF THE AGILE KANGAROO RAT (DIPODOMYS AGILIS)

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Morphologic variation between two chromosomal forms of *Dipodomys agilis* was analyzed by use of external, cranial, and bacular characters. Significant morphologic differences were evident between chromosomal forms. Discriminant-function analysis followed by examination of specimens from the Los Angeles Basin, California, suggested a broad zone of sympatry between the two chromosomal forms, primarily delineated by habitat and elevation. Animals with a diploid chromosomal number of 2n = 62 generally were collected in mesic woodland and coniferous forests at higher elevations in the San Gabriel, San Bernardino, and coastal Santa Monica mountains. Conversely, the southern chromosomal form (2n = 60) inhabits a mosaic of environments ranging from coastal grassland and chaparral in southern California to arid desert and conifer forests in Baja California. These two chromosomal forms appear to represent two distinct species.

Key words: Dipodomys, systematics, kangaroo rat, chromosomes, morphometrics, geographic variation, California, Baja California

The geographic distribution of the agile kangaroo rat (*Dipodomys agilis*) extends from the coastal mountains of southern California (35°N) through most of Baja California (25°N—Best, 1983a). The ecological distribution of this taxon ranges from sparsely vegetated deserts to montane-coniferous forests (Best, 1983a; Best et al., 1986). Although Best (1983a) summarized intraspecific variation among populations of this species, karyotypic data were unavailable for most samples. Thus, a rigorous distinction between the two chromosomal forms was not possible using morphologic criteria.

Although Best et al. (1986) documented the presence of two forms of D. agilis based on morphologic, chromosomal, and allozymic data, a large number (n = 602) of specimens from coastal-lowland basins of Los Angeles and Ventura counties were not included in their study; thus, the geographic and ecologic distribution of these two forms

in the potential zone of sympatry remains unknown. Because of their conservative interpretation of genic and morphologic data, they did not recommend species-level recognition of the northern 2n = 62 and southern 2n = 60 chromosomal forms of D. agilis. Instead, Best et al. (1986) opted to describe differences between the northern and southern populations and hypothesize that San Gorgonio Pass in southern California is the major geographic barrier separating northern and southern chromosomal forms.

Diagnostic bacula characterize many species of kangaroo rats (Best, 1981; Best and Schnell, 1974; Lidicker, 1960b). The suggestion that bacula are complex polygenic structures has led to the hypothesis that characteristics of the baculum should vary continuously and smoothly in the absence of reproductive isolation (Patterson and Thaeler, 1982). Conversely, if bacula are functional in species-specific reproduction, significant variation should exist between

closely related taxa (Patterson and Heaney, 1987: Patterson and Thaeler. 1982: Sullivan et al. 1990). Thus, if the two chromosomal forms of D. agilis represent distinct species. significant differences in characteristics of bacula should exist between populations representing the two chromosomal forms. Our objectives were to describe patterns of variation in external and cranial morphology between chromosomal forms of D. agilis using all available specimens; compare bacular morphology between chromosomal forms; test the hypothesis (Best et al., 1986) that San Gorgonio Pass in southern California is the major geographic barrier separating northern and southern chromosomal forms; assess the systematic implications of our analysis; provide a definitive statement concerning the taxonomic status of the two chromosomal forms; and propose an historical biogeographic hypothesis to explain the distribution and evolutionary relationships among species of the heermanni group of kangaroo rats.

### MATERIALS AND METHODS

Four external and 14 cranial characters (Table 1) were measured for 1,897 adult specimens from throughout the range of D. agilis (997 males, 900 females). Illustrations of characters used, methods of measuring, and aging techniques follow Best (1978, 1983a, 1993). To characterize the extent of morphologic divergence between the two karyotypic forms of D. agilis, discriminant-function analysis was performed only on populations assigned to groups based on known or probable diploid chromosomal number (2n = 62 and 2n = 60). For example, based on karyotypic investigations of Csuti (1971), Stock (1974), and Best et al. (1986), populations 1-3 were assigned to the 2n = 62 group, whereas populations 15-25 were assigned to the 2n = 60 group (Fig. 1). Because karyotypes of kangaroo rats from intervening localities (populations 4-14; Fig. 1) were largely unknown, they were not included in analyses. Upon completion of the discriminant-function analysis, however, one of us (TLB) re-examined all specimens from intervening localities. Based on diagnostic characteristics of the cranium signaled by discriminant-function analysis, as well as by visual observation, all specimens from populations 4-14 were classified as a member of either the 2n = 62 or 2n = 60 type. To test the hypothesis that San Gorgonio Pass is a major geographic barrier separating northern and southern chromosomal forms of D. agilis (Best et al., 1986), our analysis focused specifically on specimens from the heavily populated and urbanized areas lying within the lowland regions of eastern Ventura, Los Angeles, and western Riverside counties (populations 4-14). Because our morphological study included all available specimens, many of the historical collection sites predate much of the urbanization that has occurred in the region, and natural habitat in these areas may no longer exist.

Populations (Fig. 1) examined herein were as follows (population numbers corresponding to those of Best, 1983a, are in parentheses): 1, Sierra Nevada (1): 2. Mount Piños (3); 3. Santa Barbara (2 and 4): 4, Soliment Canyon (5, 6, and 9); 5, Los Angeles (7 and 10); 6, Cajon Pass (8 and 12): 7. Lake Mathews (11 and 14); 8, Cabazon (13 and 15); 9, San Luis Rey Valley (16); 10. Warner Springs (17); 11, San Diego (18); 12, Jacumba (19): 13, Ensenada (20); 14, Sierra Juarez (21): 15. Valle de Trinidad (22); 16, San Quintin Plain (23); 17, San Pedro Martir (24); 18, El Rosario (25); 19, San Agustin (26); 20, Santa Catarina (27); 21; Laguna Chapala (28); 22, San Andres (29 and 30); 23, Mesquital (31 and 32); 24, San Ignacio (33); 25, Magdalena Plain (34). A listing of specimens examined from each population is presented in Appendix I.

Bacula were prepared as outlined by Lidicker (1960b). We followed the criteria of Best and Schnell (1974) in determining age of animals and only adults were used in our analyses. Greatest length of shaft, height at base of shaft, height at mid-shaft, width at base of shaft, width at mid-shaft, width at tip of shaft, depth of tip of shaft, and angle of tip were recorded from each baculum. Camera-lucida images magnified 12× were measured to the nearest 0.01 mm with dial calipers and angles were measured to the nearest 0.5° with a protractor.

Statistical analyses were performed by use of BIO∑TAT I and II computer packages (Pimentel and Smith, 1986a, 1986b). Averages and standard deviations were computed for morphologic characters for each sex in each chromosomal group. Morphologic values were transformed to their natural logarithm following Pimentel

Table 1.—Single-classification analysis of variance (ANOVA) of differences in external and cranial characters among specimens of the 2n=62 chromosomal group (sexes combined) and the 2n=60 chromosomal group (sexes combined) of Dipodomys agilis. Average ( $\pm 1$  SD) are in parentheses and degrees of freedom are: 1,890 (males and females), 1,992 (males), and 1,884 (females), respectively. Sample size (n) for the 2n=62 and 2n=60 chromosomal groups are n=314 and n=1,551, respectively. Specimens with missing data were not included in statistical analyses.

Character	Average $(\pm 1 SD)$ for sexes combined			Average $(\pm 1 SD)$ for males			Average (±1 SD) for females		
	2n = 62	2n = 60	F-ratio	2n = 62	2n = 60	F-ratio	2n = 62	2n = 60	F-ratio
Length of body	118.4 (9.9)	114.2 (6.1)	53.1***	120.2 (9.3)	115.0 (6.6)	82.8***	116.4 (10.3)	113.3 (5.4)	6.4***
Length of tail	179.6 (10.6)	169.0 (11.1)	231.6***	181.1 (10.5)	170.3 (11.0)	114.1***	177.9 (10.3)	167.5 (11.0)	106.6***
Length of hind foot	43.6 (1.8)	41.4 (1.5)	529.6***	43.8 (1.9)	41.6 (1.6)	278.6***	43.3 (1.7)	41.1 (1.4)	296.5***
Length of ear	16.6 (2.1)	14.6 (2.1)	261.8***	17.1 (2.0)	14.7 (2.1)	163.3***	16.2 (1.9)	14.4 (2.1)	115.1***
Basal length of cranium	22.7 (0.7)	21.7 (0.6)	745.5***	22.8 (0.7)	21.8 (0.6)	455.0***	22.5 (0.7)	21.6 (0.6)	238.1***
Greatest length of cranium	39.8 (1.1)	39.1 (1.0)	124.1***	40.1 (1.0)	39.3 (1.0)	91.4***	39.5 (1.1)	38.8 (1.0)	49.0***
Maxillary arch spread	21.3 (0.9)	20.7 (0.8)	170.2***	21.5 (0.9)	20.8 (0.7)	104.4***	21.1 (0.8)	20.6 (0.8)	72.8***
Interorbital width	10.5 (0.5)	10.5 (0.6)	3.2	10.6 (0.5)	10.6 (0.7)	0.1	10.4 (0.5)	10.5 (0.5)	6.1*
Nasal length	14.7 (0.6)	14.0 (0.5)	317.9***	14.7 (0.6)	14.1 (0.5)	206.1***	14.6 (0.7)	13.9 (0.6)	135.2***
Intermaxillary width	7.4 (0.2)	7.4 (0.3)	7.2**	7.4 (0.3)	7.4 (0.3)	4.5*	7.4 (0.2)	7.3 (0.3)	3.4
Length of alveolar toothrow	5.0 (0.2)	4.9 (0.3)	6.7**	5.0 (0.3)	4.9 (0.3)	4.3*	4.9 (0.2)	4.9 (0.3)	2.9
Lacrimal length	3.7 (0.3)	3.6 (0.3)	85.4***	3.7 (0.2)	3.6 (0.3)	46.3***	3.7 (0.3)	3.6 (0.3)	42.1***
Maxillary arch width	5.0 (0.3)	4.9 (0.3)	14.0***	5.0 (0.3)	4.9 (0.3)	16.2**	4.9 (0.3)	4.8 (0.3)	1.5
Basioccipital length	5.6 (0.3)	5.6 (0.3)	2.9	5.7 (0.3)	5.6 (0.3)	0.9	5.6 (0.3)	5.6 (0.3)	2.2
Greatest depth of cranium	13.2 (0.3)	13.2 (0.3)	0.9	13.3 (0.3)	13.3 (0.3)	0.2	13.1 (0.3)	13.2 (0.3)	2.4
Greatest width of cranium	24.2 (0.7)	24.7 (0.8)	45.4***	24.5 (0.7)	24.6 (0.8)	14.3***	24.0 (0.7)	24.4 (0.7)	32.7***
Zygomatic width	19.6 (0.7)	18.9 (0.7)	283.3***	19.6 (0.6)	19.0 (0.7)	171.7***	19.5 (0.7)	18.8 (0.6)	120.0***
Nasal width	3.9 (0.2)	3.7 (0.2)	331.5***	4.0 (0.2)	3.7 (0.2)	202.5***	3.9 (0.2)	3.7 (0.2)	139.9***

<sup>\*</sup> P < 0.05; \*\* P < 0.01; \*\*\* P < 0.001.

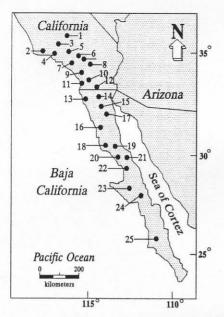


Fig. 1.—Populations of *Dipodomys agilis* sampled in southern California and Baja California: 1, Sierra Nevada; 2, Mount Piños; 3, Santa Barbara; 4, Soliment Canyon; 5, Los Angeles; 6, Cajon Pass; 7, Lake Mathews; 8, Cabazon; 9, San Luis Rey Valley; 10, Warner Springs; 11, San Diego; 12, Jacumba; 13, Ensenada; 14, Sierra Juarez; 15, Valle de Trinidad; 16, San Quintin Plain; 17, San Pedro Martir; 18, El Rosario; 19, San Agustin; 20, Santa Catarina; 21, Laguna Chapala; 22, San Andres; 23, Mesquital; 24, San Ignacio; 25, Magdalena Plain. Dots indicate the approximate geographic center of each population.

(1979) and Humphries et al. (1981). Sexual dimorphism in size was assessed within each chromosomal form by use of multivariate analysis of variance (MANOVA) followed by a single-classification analysis of variance (ANOVA) of each character. MANOVA also was used to test the equality of group centroids between specimens of the same sex, but different chromosomal groups. Standard discriminant-function analysis distinguished (on the basis of external and cranial morphology) between the two chromosomal forms of D. agilis and D. stephensi in the potential zone of sympatry. Canonical-variate analysis (CV) was used as an ordination technique to examine generalized distances and evaluate geographic variation among group centroids in reduced space (Pimentel and Smith, 1986b). Lat-

itude was related to morphologic variation by using scores of individuals (dependent variables) along CVI in a regression analysis against latitude (independent variable). Because of multiple Y-values (scores of individuals) for each X-value (latitude), a complete regression analysis is possible (Pimentel and Smith, 1986b). To test the hypothesis that interlocality variation was associated primarily with environmental variation. population centroids along CVI were used in a correlation analysis to examine the degree that morphology was reflected in a major gradient of environmental variation associated with macrohabitat diversity (Brown, 1982), average annual rainfall, and temperature (Pimentel and Smith, 1986b; Rotenberry, 1978).

Herein, we describe morphologic differences between two chromosomal forms of D. agilis; however, an additional species of kangaroo rat (D. stephensi) is sympatric-syntopic with these two chromosomal forms. Although habitat affinities of D. stephensi generally include areas of sparse vegetation, level or rolling topography, and soil neither extremely dense nor largely sand (Grinnell, 1922; Lackey, 1967), the morphologic relationship of D. stephensi to the two chromosomal forms of D. agilis is unknown. A potential criticism of our analysis is that some of the specimens we originally examined from the Los Angeles Basin may be D. stephensi, not D. agilis (Best et al., 1986). To address this issue, discriminant-function analysis of external and cranial characters was performed on each sex of D. agilis both chromosomal forms combined) and D. stephensi.

#### RESULTS

Morphologic variation.—Results of discriminant-function analysis demonstrate virtually complete separation of D. stephensi from D. agilis. Among males, 100% of D. agilis and 97% of D. stephensi were classified correctly (F = 42.4, d.f. = 18,1000; P < 0.001); for females, the range was from 100 (D. agilis) to 65% (D. stephensis), F = 31.6, d.f. = 18,893; P < 0.001). Results of the morphometric analysis of D. agilis showed that the 2n = 62 chromosomal form was distinctly larger than the 2n = 60 chromosomal group in overall external and cranial morphology (sexes combined; Fig. 2). MANOVA

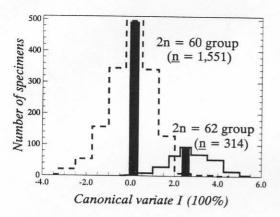


Fig. 2.—Histogram of the distribution of *Dipodomys agilis* (sexes combined) along the first canonical-variate axis of external and cranial morphology grouped by diploid (2n) number of chromosomes.

showed highly significant (F = 123.5, d.f.= 18,1000, P < 0.001) morphologic variation between specimens assigned to each chromosomal group. Discriminant-function (DF) analysis correctly classified 82 (2n = 62) and 96% (2n = 60) of the specimens to their respective karyotypic groups. The canonical correlation (r) between groups and individuals was 0.74 indicating high goodness-of-fit among individuals within each chromosomal group. Pooled-within group correlations between DFI and discriminating variables were highest for length of hind foot (0.49) and basal length of cranium (0.58). ANOVA revealed significant morphologic heterogeneity between chromosomal groups in all characters except interorbital width, basioccipital length, and greatest width of cranium (Table 1).

Within the 2n = 62 chromosomal group, MANOVA was significant (F = 2.95, d.f. = 18,322, P < 0.001) and F-values produced by ANOVA showed that means for most characters were significantly different between sexes; males were significantly larger than females in 15 (83%) of 18 characters. Discriminant-function analysis correctly assigned 67 (males) and 61% (females) of the specimens to their respective sex. Similarly, within the 2n = 60 chro-

mosomal form, MANOVA also showed significant dimorphism in size between sexes (F = 5.4, d.f. = 18,1000, P < 0.001). F-values produced by ANOVA showed that means for most characters were significantly different between sexes; males were significantly (P < 0.05) larger than females in 11 (61%) of the characters. Discriminant-function analysis of all characters simultaneously correctly assigned 68 (males) and 52% (females) of specimens to their respective sex. Thus, in both chromosomal groups, males averaged larger than females in most characters.

Significant variation in morphology also was evident between kangaroo rats of the same sex, but different karyotype. For example, MANOVA was significant (F =66.1, d.f. = 18,975, P < 0.001) when males of the 2n = 62 chromosomal group were compared to males in the 2n = 60 chromosomal group. A similar pattern of variation also was observed when females of each chromosomal group were compared (F = 59.9, d.f. = 18,867, P < 0.001). Ninety-four percent of males and females were correctly classified to their respective chromosomal form. Canonical correlation (r) between groups and individuals was 0.74 for males and 0.75 for females. Pooled within-group correlations between the first canonical-variate axis and discriminating variables were highest for length of hind foot (0.48 males and 0.52 females) and basal length of cranium (0.61 males and 0.55 females). ANOVA revealed significant morphologic heterogeneity between genders of each chromosomal form in all characters except interorbital width, intermaxillary width, length of alveolar toothrow, and greatest depth of cranium (Table 1).

Finally, specimens were grouped by sex and karyotype (four groups). As predicted, MANOVA revealed significant (F = 30.6, d.f. = 54,1000, P < 0.001) morphologic differences among groups. The first canonical variate showed a gradation in overall size from small (females of 2n = 60) to large (males of 2n = 62) among the four

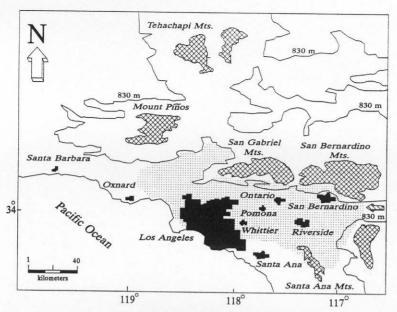


Fig. 3.—Geographic distribution of specimens assigned to the two chromosomal forms of *Dipodomys agilis* in the hypothesized zone of sympatry (stippled area) as predicted by discriminant-function analysis followed by visual evaluation of characters identified as diagnostic to each chromosomal form. Distribution of the 2n = 62 chromosomal form is generally above the 800-m contour interval, whereas distribution of the 2n = 60 chromosomal form is generally below the 800-m interval. Contemporary distribution of Petran Montane Conifer Forest is crosshatched. Metropolitan areas (black) occupied by each city encompass a region where the human population is >20,000. Arrow indicates the general region of San Gorgonio Pass:

groups evaluated by karyotype and sex. An average of 57% of the specimens were correctly classified to their respective gender and karyotype (minimum 46% for females of 2n = 62, maximum 64% for males of 2n = 60). Females of each chromosomal form were most frequently misclassified with males of the same karyotype.

Specimens of unknown karyotype.—A total of 998 individuals (522 males and 476 females) of unknown karyotype also were examined. Of these, 112 males and 101 females were assigned by visual observation of diagnostic skull characters, to the 2n = 62 group, and 410 males and 375 females were assigned to the 2n = 60 group. These data were then overlaid onto a map of the geographic distribution of the species. Contrary to Best et al. (1986), our analysis suggests a broad zone of sympatry between the two chromosomal forms (Fig. 3). This zone

encompasses virtually the entire expanse of lowland or basin habitat extending south from southern Ventura Co. near Oxnard (119°), to southern Los Angeles, Orange, southwestern San Bernardino, and northwestern Riverside counties near San Gorgonio Pass (117°). This area lies within the Californian Valley Grassland and Coastalscrub biotic communities of the Southwest (Brown, 1982).

Based on these data, we hypothesize that the 2n = 62 chromosomal form of D. agilis generally is distributed above 800 m in the San Bernardino (population 8), San Gabriel (7), and Santa Monica (9) mountains. With few exceptions, the 2n = 60 chromosomal form occurs in lowland-scrub and coastal-mountain habitat below ca. 800 m in the San Fernando Valley and Los Angeles Basin south into Baja California. Populations with both karyotypes are hypothesized to

occur primarily along the lower-elevation regions of Cajon Pass, separating the San Gabriel and San Bernardino mountains north of the city of San Bernardino, and the foothills north of the cities of San Fernando, Filmore, and Beverly Hills. Many specimens used in our analysis were collected from areas that currently lie within major metropolitan regions (e.g., Los Angeles, San Bernardino, Riverside), and many of these specimens were collected >50 years ago. Suitable natural habitat, as well as viable populations in many of these areas, likely no longer exists, thus potentially precluding future tests of reproductive isolation and detailed karyotypic assessments of animals in this highly populated and urbanized region. Further, because some collectors provided only the nearest city as the specific sampling site, the ecologic separation of the two forms may be more pronounced than indicated in Fig. 3.

Bacular morphology.—To test our hypothesis based on external and cranial characters, we also assessed variation in morphology of the baculum between the two chromosomal forms. Specimens from populations 1-3 were assigned to the 2n = 62karyotype (n = 25) and specimens from populations 15-28 were assigned to the 2n = 60 karyotype (n = 119) following the rationale described for external and cranial characters. As expected, MANOVA was significant (F = 6.9, d.f. = 8,135, P <0.001) and ANOVA showed that the 2n =62 chromosomal form is significantly ( $P \ge$ 0.05) larger than the 2n = 60 form in greatest length of shaft ( $\bar{X} = 10.78$  and 10.35 mm, respectively), height at base of shaft (1.82 and 1.72 mm) and height at mid-shaft (0.84 and 0.78 mm); whereas the 2n = 60chromosomal form has a significantly greater angle at the tip of the baculum (86.6 and 84.4°).

Geographic variation within chromosomal forms.—A test of the equality of group centroids was significant (MANO-VA; F = 4.7, df = 90,1547; P < 0.001), thus rejecting the null hypothesis of no sig-

nificant geographic variation in morphology among populations composing the 2n = 62chromosomal form (sexes combined). Discriminant-function analysis correctly classified an average of 52% of the specimens to their respective populations (range = 19% for the San Bernardino Mountains to 71% for Soliment Canyon). ANOVA revealed significant (P < 0.01) morphologic heterogeneity among populations in all characters except length of body (F = 1.6; d.f. = 5,335; P = 0.17) and length of alveolar toothrow (F = 1.03; d.f. = 5,335; P= 0.40). The first three canonical vectors accounted for 87% of the variation; two distinct groups were shown (Fig. 4a). The first group includes populations from the Sierra Nevada Mountains, Mount Piños, and the Los Angeles (San Gabriel Mountains, San Fernando Valley) areas, which plot above the origin in Fig. 4a. These populations consist of relatively large-sized and robust animals inhabiting upper to high elevations within the Sierra Montane Conifer Forest and Woodland biotic communities (Brown, 1982). The second group includes populations consisting of rather homogenous small to intermediate-sized animals, which plot below the origin in Fig. 4a. These kangaroo rats generally are found within Californian coastal-scrub and mountain habitats below ca. 500 m in the northcentral region of the Los Angeles Basin (Soliment Canyon area, Santa Clara River, Mint Canyon, Santa Monica Mountains), as well as populations inhabiting lower-elevation Californian Chaparral and Valley Grassland biotic communities in the vicinity of Santa Barbara (Santa Barbara, Lompoc, Santa Ynez) and Cajon Pass (Cajon Pass, San Bernardino Mountains, Reche Canyon).

For the 2n = 60 chromosomal form (sexes combined), MANOVA also indicated significant geographic variation among populations (F = 7.6; d.f. = 378,20790; P < 0.001). Discriminant-function analysis correctly classified an average of 34% (range = 2% for Ensenada to 69% for Valle de Trinidad) of specimens to their respec-

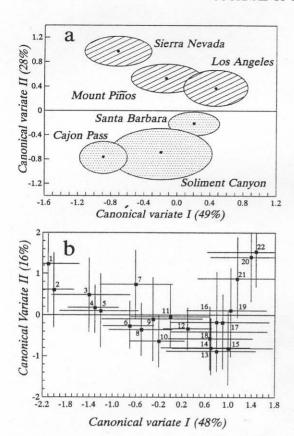


Fig. 4.—a) Two-dimensional plot of morphologic relationships among populations of the 2n = 62, and b) 2n = 60 chromosomal forms of Dipodomys agilis based on canonical discriminant-function analysis. Points represent population centroids surrounded ± 1 SD around the average (Patterson et al., 1990): 1, Sierra Nevada; 2, Mount Piños; 3, Santa Barbara; 4, Soliment Canyon; 5, Los Angeles; 6, Cajon Pass; 7, Lake Mathews; 8, Cabazon; 9, San Luis Rey Valley; 10, Warner Springs; 11, San Diego; 12, Jacumba; 13, Ensenada; 14, Sierra Juarez; 15, Valle de Trinidad; 16, San Quintin Plain; 17, San Pedro Martir; 18, El Rosario; 19, San Agustin; 20, Santa Catarina; 21, Laguna Chapala; 22, San Andres; 23, Mesquital; 24, San Ignacio; 25, Magdalena Plain.

tive populations; ANOVA showed significant (P < 0.001) morphologic heterogeneity among populations in all characters, particularly intermaxillary width (F = 17.4), length of ear (F = 14.4), and greatest length of cranium

(F = 13.8). The first three canonical vectors accounted for 75% of variation among populations. Along CVI, the distribution of population centroids showed a highly significant (r = -0.94, d.f. = 20, P < 0.001),shift in morphology along a north-to-south latitudinal gradient. Large kangaroo rats, particularly those from El Arco-San Francisquito Bay (population 20), San Ignacio (21), and Magdalena Plain (22) inhabited the southernmost latitudes; whereas small to medium-sized kangaroo rats (populations 1-19) characterized populations on northern sites. A plot of the first two canonical variate vectors showed two distinct groups (Fig. 4b). The first group was dominated by populations that showed a distinct gradation in size from small to large moving from left to right along CVI. The second group consisted of large-sized populations distributed in the extreme southernmost latitudes along the peninsula of Baja California. CVII was highly correlated with basal length of skull (0.63), intermaxillary width (0.59), length of hind foot (0.54), length of tail (0.43), and length of body (0.44).

Principal-components (PC) analysis of environmental variables associated with each population accounted for 97% of variation on the first axis. The percentage of variance of each variable contributing to PCI was 99, 92, and 38% for habitat diversity, average annual rainfall, and average annual temperature, respectively. Examination of factor loadings shows that PCI is highly correlated with habitat diversity (r =0.97), average annual rainfall (r = 0.96), and average annual temperature (r =-0.62). Thus, in the northern part of the range, high positive loadings indicate relatively moist-mild climates compared to more southern sites where conditions are warm and arid. Because virtually all of the original variability was contained in the first component, it is justifiable to treat this vector as representing an environmental gradient (Rotenberry, 1978). Further, the distribution of population centroids along CVI of morphology is significantly (r =

-0.76, n = 21) correlated with PCI of environmental variables.

### DISCUSSION

Systematic and ecologic relationships.— Chromosomal polymorphism within species of *Dipodomys* is rare; of 20 species examined, variation in diploid chromosomal number has been described for D. agilis, D. microps, D. panamintinus, and D. spectabilis (Csuti, 1971, 1979; Stock, 1974). The idea that the 2n = 62 and 2n = 60 chromosomal forms of D. agilis might represent distinct species has been alluded to based on morphologic (Best, 1983a; Huey, 1951: Lackey, 1967; Merriam, 1904), ecologic (Lackey, 1967), karyotypic (Csuti, 1971; Stock, 1974), and biochemical criteria (Best et al., 1986). Results of the present investigation demonstrate statistically significant morphologic differences between these two chromosomal forms in morphology of the baculum, crania, and external characters. Males and females of the 2n = 62 chromosomal form are significantly larger than the corresponding sex of the 2n = 60 form.

Previous chromosomal studies have not identified areas of syntopy (Wiley, 1981) between the 2n = 60 and 2n = 62 karyotypic forms (Best et al., 1986; Csuti, 1971; Stock, 1974), but examination of specimens and discriminant-function analyses of cranial and external characters suggest that sympatric associations between the two chromosomal forms exist in regions of the Los Angeles Basin. Significant differences in characteristics of the baculum between the two groups suggest the potential for reproductive isolation should the two chromosomal forms actually coexist. Further, in situations where differences in the baculum between the two groups do not coincide with species limits, the function of bacula in promoting reproductive isolation may be superseded by other isolating mechanisms. For example, ecologic factors also may contribute to reproductive isolation; the 2n = 62 form appears to inhabit more mesic habitats ranging from evergreen-woodland

to coniferous-forest. Conversely, the 2n = 60 form is ecologically eclectic, occurring in more open grassland and chaparral communities in southern California (Lackey, 1967) and ranging from desert to coniferous forest in Baja California (Best, 1983a; Best et al., 1986; Huey, 1951; Lackey, 1967; Stock, 1974).

Based on chromosomal, allozymic, morphologic, and ecologic differences between these two chromosomal forms and the morphologic separation of these two forms from D. stephensi in the hypothesized zone of sympatry (syntopy), we recommend (based on priority) that the 2n = 62 chromosomal form be referred to as D. agilis, and the 2n = 60 chromosomal form be given specific status as D. simulans. Although chromosomal and statistical techniques differentiated specimens of D. agilis and D. simulans, these two species also can be separated using diagnostic morphologic characters found on existing museum specimens. Hall (1981:575, figure 359; 1981: 577, figure 360) illustrated crania of the 2n = 62 (D. agilis) and 2n = 60 (D. simulans) taxa, respectively. Additionally, several characters reliably separate D. agilis from D. simulans, including larger size, narrower skull, and more oval-shaped auditory bullae of D. agilis as viewed from above.

## Synopsis of Subspecies

According to our findings and the conclusions of Best (1978), the correct names for the taxa of the *agilis* species complex of the *heermanni* species group in southern California and Baja California follows.

Dipodomys agilis agilis Gambel, 1848

Dipodomys agilis Gambel, 1848:77. Type locality "Pueblo de los Angeles, Upper California [= Los Angeles, Los Angeles Co., California]."

D[ipodomys]. wagneri Le Conte, 1853: 224. Type locality unknown.

Distribution.—Los Angeles Basin and foothills of San Gabriel and San Bernardino

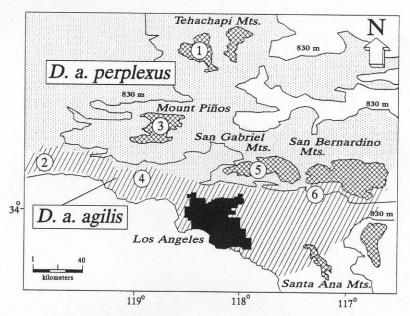


Fig. 5.—Distribution of sampled populations and subspecies within *Dipodomys agilis* (2n = 62): 1, Sierra Nevada; 2, Mount Piños; 3, Santa Barbara; 4, Soliment Canyon; 5, Los Angeles; 6, Cajon Pass. Contemporary distribution of Petran Montane Conifer Forest is crosshatched.

mountains in Ventura, Los Angeles, and Riverside counties (Fig. 5).

Remarks.—This subspecies includes specimens previously assigned to D. a. agilis, D. a. fuscus, and D. a. perplexus. Average (± 1SD) and range of external and cranial measurements (mm) are: males, character 1) 118.9(13.5) 97.0-212.0; 2) 177.2(17.5) 135.0-200.0; 3) 42.7(3.7) 37.0-47.0; 4) 16.4(2.5) 12.0-20.0; 5)22.4(1.8) 21.0-24.6; 6) 39.4(4.4) 37.8-41.9; 7) 21.1(1.9) 17.8–29.7; 8) 10.5(1.2) 9.4-20.6; 9) 14.4(1.2) 13.4-15.9; 10) 7.3(0.6) 6.8–8.0; 11) 4.9(0.5) 4.3–5.5; 12) 3.7(0.4) 2.8-4.3; 13) 4.9(0.5) 4.2-5.7; 14) 5.6(0.5) 4.7-6.2; 15) 13.1(1.1) 11.8-13.8; 16) 24.0(2.0) 22.5-25.8; 17) 19.3(1.6) 17.8-21.4; 18) 3.9(0.4) 3.2-4.5; females, character 1) 116.8(6.3) 97.0-136.0; 2) 174.7(12.0) 110–205.0; 3) 42.9(1.7) 40.0– 47.0; 4) 16.2(2.0) 11.0-20.0; 5) 22.4(0.6) 20.8-23.9; 6) 39.2(1.1) 36.5-41.9; 7) 21.0(0.8) 18.8-23.0; 8) 10.4(0.5) 9.3-11.5; 9) 14.3(0.6) 12.7-15.7; 10) 7.4(0.2) 6.8-8.1; 11) 4.9(0.2) 4.4-5.6; 12) 3.7(0.3) 291-4.4; 13) 4.9(0.3) 4.1-5.5; 14) 5.5(0.3)

4.4-6.3; 15) 13.1(0.3) 11.9-14.0; 16) 23.8(0.7) 22.0-25.9; 17) 19.3(0.7) 17.6-21.2; 18) 3.9(0.2) 3.4-4.3.

Specimens examined.—(171 males and 130 females): includes specimens listed as populations 3, 4A, and 6A in Appendix I.

# Dipodomys agilis perplexus (Merriam, 1907)

Perodipus perplexus Merriam, 1907:79. Type locality "Walker Basin, Kern Co., Calif."

Dipodomys agilis fuscus Boulware, 1943:393. Type locality "2½ mi. N La Purisima Mission, 600 ft., Santa Barbara County, California."

Distribution.—Southern Sierra Nevada including Mount Piños, Tehachapi and San Gabriel mountains, and northern San Fernando Valley. This is the northernmost subspecies of *D. agilis* (Fig. 5).

Remarks.—This subspecies includes specimens previously assigned to D. a. agilis and D. a. perplexus. Average (± 1SD) and range of external and cranial measurements (mm) are: males, character 1)

119.6(7.2) 81.0-140.0; 2) 183.1(12.9) 109.0-230.0; 3) 44.5(1.9) 37.0-50.0; 4) 17.6(2.1) 10.0-22.0; 5) 22.9(0.6) 24.4-24.6; 6) 40.3(1.0) 36.5-42.9; 7) 21.6(0.8) 19.1-23.5; 8) 10.5(0.6) 9.4-11.9; 9) 14.8(0.6) 12.6-16.0; 10) 7.4(0.3) 6.8-8.1; 11) 5.0(0.3) 4.5-5.7; 12) 3.8(0.3) 3.0-4.9; 13) 5.0(0.3) 4.3-5.8; 14) 5.7(0.3) 4.8-6.5; 15) 13.4(0.3) 12.4-15.6; 16) 24.4(0.7) 21.1-25.7; 17) 19.8(0.7) 18.2-21.3; 18) 4.0(0.2) 3.5-4.5; females, character 1) 117.8(8.3) 90.0-173.0; 2) 181.1(10.3) 118.0-203.0; 3) 43.9(1.7) 38.0-48.0; 4) 16.8(1.8) 13.0-21.0; 5) 22.8(0.6) 21.1-24.6; 6) 39.9(1.0) 37.8-42.6; 7) 21.4(0.7) 19.5-23.0; 8) 10.4(0.5) 9.0-11.5; 9) 14.8(0.6) 13.3-16.4; 10) 7.4(0.2) 6.8-8.2; 11) 5.0(0.2) 4.5-5.5; 12) 3.8(0.3) 3.1-4.7; 13) 5.0(0.3) 4.2-5.7; 14) 5.7(0.3) 5.0-6.3; 15) 13.3(0.3) 12.6-13.9; 16) 24.3(0.5) 23.0-25.4; 17) 19.7(0.7) 17.9-21.8; 18) 3.9(0.2) 3.4-4.4.

Specimens examined.—(177 males and 133 females): includes specimens listed as populations 1, 2, and 5A in Appendix I.

# Dipodomys simulans simulans (Merriam, 1904)

Perodipus streator simulans Merriam, 1904:144. Type locality "Dulzura, San Diego Co., California."

Perodipus cabezonae Merriam, 1904: 144. Type locality "Cabezon, Colorado Desert [Riverside Co.], California."

Dipodomys agilis latimaxillaris Huey, 1925:84. Type locality "2 miles west of Santo Domingo Mission, Lower California, Mexico, lat. 30°45′ north, long. 115°58′ west—or precisely, alluvial river bottom near the huge red cliff that marks the entrance to the Santo Domingo River canyon from the coastal plain."

Dipodomys agilis martirensis Huey, 1927:7. Type locality "La Grulla, (east side of valley), Sierra San Pedro Martir, Lower California, Mexico, altitude 7,500 feet."

Dipodomys agilis plectilis Huey, 1951: 240. Type locality "mouth of canyon San

Juan de Dios, lat. 30°07'N, Baja California."

Dipodomys paralius Huey, 1951:241. Type locality "Santa Catarina Landing (Lat. 29°31'N). Baja California, Mexico."

Dipodomys peninsularis pedionomus Huey, 1951:247. Type locality "2 miles north of Chapala Dry Lake, on Llano de Santa Ana, lat. 29°30′N., long. 114°35′W., Baja California, Mexico."

Dipodomys peninsularis eremoecus Huey, 1951:248. Type locality "7 miles west of San Francisquito Bay, lat. 28°30'N., Gulf of California, Baja California, Mexico."

Dipodomys peninsularis australis Huey, 1951:249. Type locality "Santo Domingo, Magdalena Plain, Baja California, Mexico, lat. 25°30'N."

Dipodomys antiquarius Huey, 1962:477. Type locality "San Juan Mine, Sierra San Borja, Baja California, Mexico, alt. 4,000 feet, lat. 28°41'N., long. 113°37'W."

Distribution.—Southern California to middle Baja California (Fig. 6).

Remarks.—Average (± 1SD) and range of external and cranial measurements (mm) are: males, character 1) 114.5(7.4) 56.0-171.9; 2) 170.1(11.3) 110–213; 3) 41.5(1.7) 23.0-48.0; 4) 14.8(2.1) 9.0-27.0; 5) 21.7(0.6) 19.1-23.8; 6) 39.3(0.9) 35.7-42.7; 7) 20.7(0.8) 14.0-24.7; 8) 10.5(0.6) 8.7-19.8; 9) 14.1(0.5) 12.5-16.7; 10) 7.3(0.2) 6.7–8.2; 11) 4.9(0.3) 4.2–5.8; 12) 3.6(0.3) 2.4-5.3; 13) 4.9(0.3) 4.0-6.8; 14) 5.6(0.3) 4.4-6.6; 15) 13.2(0.3) 12.0-14.3; 16) 24.4(0.7) 22.2–26.6; 17) 18.9(0.7) 16.8-22.1; 18) 3.7(0.2) 3.0-4.4; females, character 1) 113.3(5.7) 79.0-135.0; 2) 167.7(11.1) 108-196.03) 41.3(1.5) 29.0-49.0; 4) 14.6(2.0) 11.0-20.0; 5) 21.5(0.6) 19.1-23.4; 6) 38.7(1.1) 21.3-42.4; 7) 20.5(0.8) 18.1–24.3; 8) 10.5(0.5) 8.8–12.2; 9) 13.9(0.6) 7.3–15.6; 10) 7.3(0.3) 4.4–9.9; 11) 4.9(0.3) 3.7-5.9; 12) 3.5(0.3) 2.8-4.9; 13) 4.9(0.3) 3.0-6.3; 14) 5.6(0.3) 4.5-6.7; 15) 13.2(0.3) 12.3–14.0; 16) 24.2(0.6) 22.2-26.6; 17) 18.8(0.7) 16.7-21.5; 18) 3.7(0.2) 2.9-4.4.

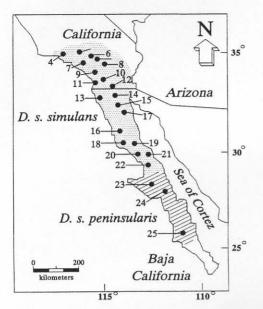


FIG. 6.—Distribution of sampled populations and subspecies within *Dipodomys simulans* (2n = 60): 4, Soliment Canyon; 6, Cajon Pass; 7, Lake Mathews; 8, Cabazon; 9, San Luis Rey Valley; 10, Warner Springs; 11, San Diego; 12, Jacumba; 13, Ensenada; 14, Sierra Juarez; 15, Valle de Trinidad; 16, San Quintin Plain; 17, San Pedro Martir; 18, El Rosario; 19, San Agustin; 20, Santa Catarina; 21, Laguna Chapala; 22, San Andres; 23, Mesquital; 24, San Ignacio; 25, Magdalena Plain.

Specimens examined.—(1,220 males and 996 females): includes specimens listed as populations 4S, 5S, 6S, 7S, 8S, and 9-24 in Appendix I.

### Dipodomys simulans peninsularis (Merriam, 1907)

Perodipus simulans peninsularis Merriam, 1907:79. Type locality "Santo Domingo [lat. 28° 15'—Huey, 1951], Lower California, Mexico."

Dipodomys peninsularis peninsularis, Huey, 1951:246, see above.

Distribution.—Southern Baja California (Fig. 6).

Remarks.—We are not aware of any major geographic barriers that separate this rather large form from D. s. simulans. Average ( $\pm$  1SD) and range of external and

cranial measurements (mm) are: males, character 1) 115.2(6.0) 105.0-136.0; 2) 170.2(10.0) 150.0-198.0; 3) 42.5(1.7) 40.0-47.0; 4) 15.8(2.8) 12.0-21.0; 5) 22.8(0.6) 20.2-23.4; 6) 40.2(1.0) 37.8-42.2; 7) 21.8(0.8) 19.0-23.2; 8) 11.6(0.5) 9.6-12.0; 9) 15.2(0.5) 12.9-15.6; 10) 8.4(0.3) 7.0-8.3; 11) 6.0(0.2) 4.3-5.8; 12) 4.7(0.2) 3.1-4.3; 13) 6.0(0.3) 4.3-5.7; 14) 6.7(0.3) 5.0-6.4; 15) 14.3(0.3) 12.6-14.4; 16) 25.5(0.8) 23.6-26.9; 17) 20.0(0.6) 18.1-20.8; 18) 4.8(0.2) 3.2-4.3; females, character 1) 117.0(5.5) 104.0-131.0; 2) 172.1(10.5) 145.0-198.0; 3) 42.5(1.5) 40.0-46.0; 4) 15.4(2.7) 11.0-19.0; 5) 21.9(0.6) 20.3-23.4; 6) 39.9(0.9) 36.8-42.2; 7) 21.2(0.8) 18.6-22.8; 8) 10.6(0.5) 9.3-11.9; 9) 14.1(0.5) 12.9-15.3; 10) 7.6(0.2) 7.0-8.2; 11) 5.1(0.3) 4.3-5.7; 12) 3.7(0.2) 2.9-4.3; 13) 5.0(0.3) 4.3-5.8; 14) 5.7(0.3) 5.0-6.2; 15) 13.6(0.4) 12.6-14.4; 16) 25.4(0.8) 23.2-26.9; 17) 19.2(0.6) 17.1-20.5; 18) 3.7(0.2) 3.1-4.2.

Specimens examined.—(134 males and 128 females): includes specimens listed as populations 25 and 26 in Appendix I.

## Historical Biogeographic Hypothesis

A Matthewian model (Murphy, 1983b) has been proposed to explain contemporary patterns of distribution and differentiation of vertebrates on peninsular Baja California. It represents variations on a theme that derive peninsular biotas from northern ancestors that dispersed southward from southern California and Arizona. Alternatively, the transgulfian vicariance hypothesis (Murphy, 1983a, 1983b) states that many unique species in Baja California evolved in isolation when the peninsula separated from the mainland of Mexico during the Miocene  $(1.5 \times 10^7 \text{ years ago})$ .

Fossils referable to the genus *Dipodomys* are known from the Miocene to Recent of western North America, yet extant species appear to have arisen since the early Pleistocene from an ancestral lineage that included the genus *Prodipodomys* (Hafner and Hafner, 1983). Sympatric occurrences

of fossil *Dipodomys* and *Prodipodomys* are known from the Colorado Desert of southern California from early to middle Pleistocene (Hafner and Hafner, 1983). The transgulfian vicariance hypothesis, therefore, does not appear to be appropriate for predicting patterns of speciation in kangaroo rats because separation of the peninsula from mainland Sonora occurred too early.

During late Pliocene to early Pleistocene, the Los Angeles Basin was inundated by the sea, and orogeny of the Sierra Nevada and Coast ranges was just beginning (Smith, 1979). Flooding and the northern extension of the Sea of Cortez prevented or severely restricted dispersal along the mesic corridor of the Baja California peninsula at its northern limit (Murphy, 1983a, 1983b). At this time, the San Gorgonio Pass is hypothesized to have acted as a filter barrier. preventing sympatry between populations of xeric-adapted vertebrates to the north and south. By late Pliocene, the mid-peninsular desert had formed and isolated mesic-adapted taxa to the south and north. During the Pleistocene, the Sea of Cortez receded to its present location, eliminating the San Gorgonio Barrier. During the late Pleistocene, Lake Coahuilla (Coachella Valley) occupied a considerably larger part of the Imperial Valley than is occupied presently by the extant Salton Sea (Durham and Allison, 1960). Presumably much of the Los Angeles Basin also was inundated by ocean at this time. By early to middle Pleistocene, the presumed ancestral stock of the heermanni group of kangaroo rats penetrated the Colorado and Mojave deserts and spread throughout the Great Basin, California, and Baja California (Stock, 1974). Based on inferences derived from karyology and morphology, Stock (1974) hypothesized that this ancestral form is represented best by two extant species, D. gravipes and D. stephensi. Accordingly, these species represent relic sister taxa, with D. stephensi becoming isolated in the San Luis Rey, San Jacinto, and San Bernardino valleys as a result of the last major mountain-building activity in the middle Pleistocene, as postulated by Lidicker (1960a) for *D. merriami*.

Dipodomys gravines currently inhabits a small area of lowland-coastal scrub south of San Telmo to near El Rosario, Baia California (Best, 1983b). During the Pleistocene interglacials, the vegetation of the Mojave Desert extended southward between the Sierra Juarez and Sierra San Pedro Martir and the northwestern gulf coast (Cody et al., 1983). Such an intrusion of desert vegetation could have isolated the ancestral lineage that gave rise to D. gravines. Based on the degree of morphologic differentiation between D. gravipes and D. stephensi, Lackey (1967) hypothesized that these two taxa have been isolated for a period much longer that 6,000 years.

Drawing inferences from morphology and ecology, Lackey (1967) hypothesized that the narrow-faced group (including D. agilis) was derived from an arid-dwelling heermanni form, probably in Baja California, that subsequently invaded the chaparral community along the Pacific region of California. Stock (1974) interpreted Lackey's (1967) statements as meaning that the narrow-faced subgroup was derived from a wide-faced form, and that D. agilis was an early offshoot of this ancestral lineage. Stock (1974) argued on karyotypic grounds, however, that D. agilis was derived from the common ancestor that produced D. heermanni, or directly from D. heermanni or D. panamintinus. D. agilis and D. simulans are distinct from D. gravipes and D. stephensi, but can be derived from D. heermanni by incorporation of one centric fusion and several pericentric inversions (Stock, 1974).

If an ancestral *heermanni* stock gave rise to a mesic-adapted population of kangaroo rats in the southern Sierra Nevada Mountains (D. agilis, 2n=62) that subsequently dispersed across San Gorgonio Pass and along the corridor of mesic vegetation that stretched along the northern peninsular region during early Pleistocene, formation of the mid-peninsular desert may have isolated

the ancestral stock that ultimately gave rise to D. simulans (2n = 60). The contemporary distribution of this species in Baja California includes mesic, chaparral, and arid-lowland habitats. A similar paleobiogeographic hypothesis also has been implicated in the patterns of differentiation exhibited by northern and southern subspecies of *Peromyscus californicus* (Smith, 1979).

The eastern limit of the distribution of D. agilis and D. simulans borders the Coachella Valley north of the Salton Sea along the western edge of the Mojave Desert. If San Gorgonio Pass represents a filter barrier separating the San Bernardino from the San Jacinto mountains, dispersal by D. simulans from Baja California most likely occurred along a coastal corridor from Baja California through San Diego Co., into the present Pacific-lowland basin of Los Angeles Co., where it is now sympatric with D. agilis and D. stephensi. Lackey (1967) indicated that in the region of Cajon Pass, separating the San Gabriel and San Bernardino mountains, D. panamintinus and D. stephensi occur together. Our analysis indicates that D. agilis and D. simulans also inhabit this region.

### ACKNOWLEDGMENTS

We thank R. G. Hannum (R. G. Hannum Collection) and S. B. George (Los Angeles County Museum) for allowing us to remove and prepare bacula from specimens in their collections, personnel at the museums listed in Appendix I for providing access to specimens, and F. S. Dobson, R. S. Lishak, R. E. Mirarchi, and S. A. Smith for providing suggestions that significantly improved the manuscript. This is journal article 15-892236P of the Alabama Agricultural Experiment Station.

### LITERATURE CITED

- BEST, T. L. 1978. Variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Journal of Mammalogy, 59:160–175.
- . 1981. Bacular variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. The Southwestern Naturalist, 25:529–534.
- —. 1983a. Intraspecific variation in the agile

- kangaroo rat (*Dipodomys agilis*). Journal of Mammalogy, 64:426-436.
- ——. 1983b. Morphologic variation in the San Quintin kangaroo rat (Dipodomys gravipes Huey 1925). The American Midland Naturalist, 109: 409–413.
- ——. 1993. Patterns of morphologic and morphometric variation in heteromyid rodents. Pp. 197–235, in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists, 10:1–719.
- BEST, T. L., AND G. D. SCHNELL. 1974. Bacular variation in kangaroo rats (genus Dipodomys). The American Midland Naturalist, 91:257–270.
- BEST, T. L., R. M. SULLIVAN, J. A. COOK, AND T. L. YATES. 1986. Chromosomal, genic, and morphologic variation in the agile kangaroo rat, *Dipodomys agilis* (Rodentia: Heteromyidae). Systematic Zoology, 35:311–324.
- BOULWARE, J. T. 1943. Two new subspecies of kangaroo rats (genus Dipodomys) from southern California. University of California Publications in Zoology, 46:391–396.
- Brown, D. E. 1982. Biotic communities of the American-United States and Mexico. Desert Plants, 4:1–342.
- Cody, M. L., R. Morgan, and H. Thompson. 1983. The plants. Pp. 49–97, *in* Island biogeography in the Sea of Cortez (T. J. Case and M. L. Cody, eds.). University of California Press, Berkeley, 508 pp.
- CSUTI, B. A. 1971. Karyotypes of kangaroo rats from southern California. Journal of Mammalogy, 52: 202–206.
- ——. 1979. Patterns of adaptation and variation in the Great Basin kangaroo rat (*Dipodomys microps*). University of California Publications in Zoology, 111:1–69.
- Durham, J., and E. C. Allison. 1960. The geographic history of Baja California and its marine faunas. Systematic Zoology, 9:47–91.
- GAMBEL, W. 1848. Descriptions of two new California quadrupeds. Proceedings of the Academy of Natural Sciences of Philadelphia, 4:77–78.
- GRINNELL, J. 1922. A geographical study of the kangaroo rats of California. University of California Publications in Zoology, 24:1–124.
- HAFNER, J. C., AND M. S. HAFNER. 1983. Evolutionary relationships of heteromyid rodents. Great Basin Naturalist Memoirs, 7:3–29.
- Hall, E. R. 1981. The mammals of North America. John Wiley & Sons, New York, 1:1-600 + 90.
- HUEY, L. M. 1925. Two new kangaroo rats of the genus Dipodomys from Lower California. Proceedings of the Biological Society of Washington, 38: 83–84.
- . 1927. A discussion of the zonal status of the Sierra San Pedro Martir, Lower California, Mexico, with descriptions of a new kangaroo rat and a new woodpecker from that region. Transactions of the San Diego Society of Natural History, 5:1-10.
- ——. 1951. The kangaroo rats (Dipodomys) of Baja California, Mexico. Transactions of the San Diego Society of Natural History, 11:205–255.
- ——. 1962. Two new species of broad-faced fivetoed kangaroo rats (genus *Dipodomys*). Transactions

of the San Diego Society of Natural History, 12: 477-480.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. H. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology, 30:291–308.

LACKEY, J. A. 1967. Biosystematics of heermanni group kangaroo rats in southern California. Transactions of the San Diego Society of Natural History, 14:313–344.

LE CONTE, J. L. 1853. Remarks on the genus Dipodomys and Perognathus. Proceedings of the Academy of Natural Sciences of Philadelphia. 6:224–225.

LIDICKER, W. Z., JR. 1960a. An analysis of intraspecific variation in the kangaroo rat Dipodomys merriami. University of California Publications in Zoology, 67:125–218.

and its implications for superspecific groupings of kangaroo rats. Journal of Mammalogy, 41:495–499.

Merriam, C. H. 1904. New and little known kangaroo rats of the genus *Perodipus*. Proceedings of the Biological Society of Washington, 17:139–146.

——. 1907. Description of ten new kangaroo rats. Proceedings of the Biological Society of Washington, 20:75–79.

MURPHY, R. W. 1983a. Paleobiogeography and patterns of genetic differentiation of the Baja California herpetofauna. Occasional Papers of the California Academy of Sciences, 137:1–48.

. 1983b. The reptiles: origins and evolution. Pp. 130–158, *in* Island biogeography in the Sea of Cortez (T. J. Case and M. L. Cody, eds.). University of California Press, Berkeley, 508 pp.

PATTERSON, B. D., AND L. R. HEANEY. 1987. Preliminary analysis of geographic variation in red-tailed chipmunks (*Eutamias ruficaudus*). Journal of Mammalogy, 68:782–791.

PATTERSON, B. D., AND C. S. THAELER, JR. 1982. The mammalian baculum: hypotheses on the nature of bacular variability. Journal of Mammalogy, 63:1–15.

Patterson, B. D., P. L. Meserve, and B. K. Lang. 1990. Quantitative habitat associations of small mammals along an elevational transect in temperate rainforests of Chile. Journal of Mammalogy, 71: 620–633.

PIMENTEL, R. A. 1979. Morphometrics: the multivariate analysis of biological data. Kendall/Hunt Publishing Company, Dubuque, Iowa, 276 pp.

PIMENTEL, R. A., AND J. D. SMITH. 1986a. BIO∑TAT I: a univariate statistical toolbox. Sigma Soft, Placentia, California, 239 pp.

——. 1986b. BIO∑TAT II: a multivariate statistical toolbox. Sigma Soft, Placentia, California, 212 pp.

ROTENBERRY, J. T. 1978. Components of avian diversity along a multifactorial climatic gradient. Ecology, 58:693–699.

SMITH, M. F. 1979. Geographic variation in genic and morphologic characters in *Peromyscus californicus*. Journal of Mammalogy, 60:705–722.

SULLIVAN, R. M., S. W. CALHOUN, AND I. F. GREEN-BAUM. 1990. Geographic variation in genital morphology among insular and mainland populations of *Peromuscus maniculatus* and *Peromyscus oreas*. Journal of Mammalogy, 71:48–58.

STOCK, A. D. 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. Journal of Mammalogy, 55:505–526.

WILEY, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley & Sons, New York, 439 pp.

Submitted 28 April 1995. Accepted 25 August 1996.

Associate Editor was Karen McBee.

### APPENDIX I

Specimens examined.—Museums (with acronyms in parentheses) containing specimens of Dipodomys examined in this study are: American Museum of Natural History (AMNH); California Academy of Sciences (CAS): California State University, Long Beach (LBSU); Field Museum of Natural History (FMNH); Los Angeles County Museum of Natural History (LACM); Louisiana State University (LSU); San Diego Natural History Museum (SDNHM); South Dakota State College (SDSC); Texas A&M University, Texas Cooperative Wildlife Research Collection (TCWC): United States National Museum of Natural History (USNM): University of Arizona (UA); University of California at Berkeley. Museum of Vertebrate Zoology (MVZ); University of California at Los Angeles (UCLA); Natural History Museum of Los Angeles County (LACM); University of Illinois (UI); University of Michigan (UMMZ); University of New Mexico, Museum of Southwestern Biology (MSB); University of Kansas, Museum of Natural History (KU); University of Oklahoma Museum of Natural (UOMZ).

Population 1.—Sierra Nevada (53 males, 47 females). CALIFORNIA. KERN CO.: 1 mile SE Bodfish (LBSU 1, 1); Kernville (USNM 2, 0): 1 mile NE Lake Isabella off highway 178, 1,900 feet (LBSU 0, 1); 3½ miles E, 2¼ miles N Monolith, Sand Canyon, 4,125 feet (LACM 0, 1); Sand Creek, 4 miles N Monolith, 5,000 feet (LACM 1, 4); Piute Mountains (UMMZ 2, 0: USNM 3, 1); Rip-Rap Mine, Piute Mountains (LACM 2, 0; MVZ 1, 1); 2 miles N Sorrell's Ranch, Kelso Valley, 4,500 feet (MVZ 1, 0); South Fork Kern, Onyx (USNM 1, 0); 1.5 miles N Tehachapi, 4,250 feet (MVZ 0, 2); 8 miles SW Tehachapi (LACM 1, 0); Thompson Canyon, Walker Basin, 3,400-3,900 feet (MVZ 13, 6); 11/2 miles E, 1 mile N Twin Oaks, Black Canyon Road, Upper Caliente Creek (LACM 4, 0); Walker Basin (MVZ 2, 1; USNM 1, 4); Walker

Basin, 3,400 feet (UCLA 12, 20); SW part of Walker Basin (MVZ 5, 3). TULARE CO.: 13.4 miles N on Sierra Way from junction of Kernville Road, Sequoia National Forest (LBSU 1, 0); Trout Creek, Sierra Nevada, 6,000 feet (MVZ 0, 1).

Population 2.-Mount Piños (56 males, 46 females). CALIFORNIA. KERN CO.: Castaic Lake, Fort Tejon (FMNH 4, 0); Cuddy Valley, 5,000 feet (UCLA 1, 2); Cuddy Valley, 5,500 feet (MVZ 1, 1); Cuddy Valley, 6,500 feet (UMMZ 1, 0); head of Cuddy Valley, 5,900 feet (MVZ 1, 1); head of Cuddy Valley, 6,000 feet (MVZ 1, 3); Cuddy Valley, Mount Piños, 6,000 feet (UCLA 0, 1); Fort Tejon (FMNH 0, 1; USNM 0, 1); 6 miles W Lebec, 5,000 feet (SDNHM 7, 6); 15 miles W Lebec (LACM 1. 1); 17 miles W Lebec, Cuddy Valley, 6,000 feet (LACM 1, 1); Mount Piños, 10 miles W Lebec, 5,500 feet (UCLA 1, 0); Mount Piños (LACM 5, 6; SDNHM 1, 0; LSU 1, 1); S side Mount Piños road, 1 mile W Kern County Fire Department, Frazier Park (LACM 1, 1); Quail Lake (LACM 1, 0); San Emigdia Canyon (USNM 2, 1); Tejon Pass (USNM 0, 1). LOS ANGELES CO.: Elizabeth Lake (MVZ 1, 0); 2 miles E Gorman, 3,500 feet (MVZ 1, 0); Hughes Lake (SDNHM 0, 1); Lake Hughes (LACM 0, 1); 1 mile W Quail Lake (LACM 0, 1); Sanberg, Mount Libre (LACM 2, 1). VENTURA CO .: Cuddy Canyon (MVZ 0, 1); Cuddy Valley, 6,500 feet (LACM 2, 1); 1.5 miles S, 1.5 miles W Frazier Park in Los Padres National Forest, 5,500 feet (LBSU 0, 1); 12 miles W Lebec on Frazier Park Road (LBSU 2, 0); Lockwood Valley, 5,500 feet (UCLA 1, 0); 1/4 mile N Griffin, Lockwood Valley, 4,900 feet (MVZ 3, 0); Mount Piños, Lockwood Valley (FMNH 1, 3); Mount Piños, 5,500-6,500 feet (MVZ 5, 1; UCLA 1, 0); 1.5 miles ESE Mount Piños, 8,100 feet (MVZ 0, 1); Mount Piños, 13.1 miles W, 0.6 mile S Gorman (LBSU 3, 3); Ozena Public Camp, Los Padres National Forest (LBSU 2, 0); head Piru Creek, Mount Piños, 6,500 feet (LACM 1, 0); head of Piru River (MVZ 1, 2); ½ mile W Ventura County line, upper Canada de Alamos (LACM 0, 1).

Population 3.—Santa Barbara (27 males, 12 females). CALIFORNIA. SANTA BARBARA CO.: Carpinteria (SDNHM 3, 0); 1.5 miles N La Purisima Mission, 600 feet (MVZ 2, 1); Little Caliente Road, Mono Basin, 1,450 feet (MVZ 1, 0); 1 3/4 miles N Lompoc, C. A. Davis Ranch,

400 feet (MVZ 1, 0); Point Arguello (LACM 2, 1); 7 miles E San Marcus Pass on Camino Cielo (LBSU 1, 1); 7 miles E San Marcos Pass on El Cielo highway in Santa Ynez Mountains (LBSU 1, 0); Santa Barbara School, 2 miles E by N Carpinteria, 400 feet (MVZ 2, 5); mouth of Santa Ynez River (MVZ 3, 1). VENTURA CO.: Matilija (MVZ 3, 2); 3 miles W Ojai, 600 feet (UCLA 4, 1); Ojai Valley, vicinity of Whale Rock, 1,250 feet (UCLA 4, 0).

Population 4A.—Soliment Canyon (76 males, 63 females). CALIFORNIA. LOS ANGELES CO.: 1 mile W Acton (LACM 2, 1); 1 mile N, 2½ miles W Acton (LACM 2, 1); 1½ miles N, 3 miles W Acton, Escondito Road, 3,200 feet (LACM 2, 3); 134 miles N, 21/2 miles W Acton (LACM 0, 1); 2 miles N Acton (LACM 2, 0); 2 miles E Acton, sandy wash (LACM 1, 0); 2 miles N, 2 miles W Acton, 3,200 feet (LACM 1, 2); 2 miles NW Acton, Hubbard Canyon (LACM 1, 0); 4 miles N, 2 miles W Acton, Old Sierra Highway, 3,400 feet (LACM 1, 3); end of airport, Agua Dulce Canyon (LACM 3, 0); Castaic (SDNHM 1, 2); 3½ miles E, 2½ miles N Castaic junction, San Francisquito Canyon, 1,300 feet (LACM 0, 2); Cold Creek-Stone Canyon Road, 200 yards W junction Mulholland Highway (LACM 1, 1); Escondito Canyon (LACM 0, 1); 2 miles N freeway, Escondito Canyon (LACM 0, 1); junction Hasley Canyon and Santa Clara Valley (LACM 0, 1); Hasley Canyon, Val Verde (LACM 0, 1); 2 miles W Lang, sandy wash (LACM 0, 1); ½ mile E Lang, Santa Clara River wash (LACM 0, 2); Lang, Soliment Canyon, Santa Clara River wash (LACM 0, 1); Magic Mountain, 4,800 feet (LACM 0, 1); summit of Magic Mountain, San Gabriel Mountains (LACM 1, 1); Mint Canyon (LACM 1, 0); Mint Canyon, 2,400 feet (MVZ 2, 2); Mint Canyon, 10 miles E Sangus (LACM 1, 1); Newhall, San Francisquito Canyon Road (Sangus) (LACM 1, 0); 11/2 miles N Oaks, Mint Canyon, Rowher Flats, 2,400 feet (LACM 5, 5); Rowher Flats, Mint Canyon (LACM 0, 1); ½ mile E highway 99, Rye Canyon hillside (LACM 1, 0); 0.4 mile E highway 99, Rye Canyon (LACM 1, 0); 1.1 miles E highway 99, Rye Canyon (LACM 1, 0); 1 mile E highway 99, Santa Clara River (LACM 2, 0); Santa Monica, 500 feet (USNM 4, 1); Santa Monica Mountains (MVZ 1, 0); NE slope Saddle Peak, Santa Monica Mountains, 1,800 feet (LACM 4, 1); Sawtelle (LACM 5, 5); SDNHM 8, 5; UCLA 1, 0; USNM

5, 1); Soliment junction, Mint Canyon (LACM 0, 1); 2 miles E Soliment (LBSU 1, 0); 3 miles W Soliment junction (LACM 1, 0); 4 miles W Soliment junction (LACM 1, 0); Lang, Soledad Canyon (LACM 1, 1); ½ mile N highway 14, Spring Canyon (LACM 1, 0); highway 99 and Valencia Boulevard (LACM 0, 1); 3 miles S, 2.6 miles W junction 6 Angeles Forest highway (= Vincent) (LACM 1, 0). VENTURA CO.: 3 miles from Filmore on highway 126 (LBSU 0, 1); 4 miles E Filmore, Santa Clara Valley (LACM 0, 1); 4 miles E Filmore, Santa Clara River wash (LACM 3, 1); 4 miles E Filmore, Santa Clara River wash, 490 feet (LACM 1, 0); ½ mile W Moore State College (LACM 1, 1); 4 miles E Moorpark, highway 118, Arroyo Simi (LACM 0, 1); 21/2 miles W, 11/2 miles S Simi (LACM 1, 1); 34 mile W Somis, 150 feet (MVZ 1, 1); Little Sycamore Canyon, 7.2 miles E of coast highway 101, 1,900 feet (LBSU 2, 5).

Population 4S.—Soliment Canyon (17 males, 18 females). CALIFORNIA. LOS ANGELES CO.: end of airport, Agua Dulce Canyon (LACM 0, 1); 3½ miles E, 2½ miles N Castaic junction, San Francisquito Canyon, 1,300 feet (LACM 2, 2); junction Hasley Canyon and Santa Clara Valley (LACM 0, 1); Lang, Soledad Canyon (LACM 1, 2); ½ mile E Lang, Santa Clara River wash (LACM 0, 1); 1 mile W Lang (LACM 1, 0); Malabou Lake (CAS 1, 0); Mint Canyon, 2,400 feet (MVZ 0, 2); 1½ miles N Oaks, Mint Canyon, Rowher Flats, 2,400 feet (LACM 4, 1); 0.01 mile E highway 99, Rye Canyon, Santa Clara River bottom (LACM 1, 0); 0.4 mile E highway 99, Rye Canyon (LACM 1, 1); 1.2 miles E highway 99, Rye Canyon (LACM 2, 1); San Francisquito Canyon, 1,300 feet (LACM 0, 1); 1/2 mile E highway 99, Santa Clara River wash (LACM 0, 1); 1 mile E highway 99, Santa Clara River wash (LACM 0, 1); N slope Saddle Peak, Santa Monica Mountains. 1,800 feet (LACM 0, 1); NE slope Saddle Peak, Santa Monica Mountains, 1,800 feet (LACM 0, 1); 4 miles W Soliment junction (LACM 0, 1); Topanga Canyon, west ridge, 21/2 miles SW Woodland Hills (LBSU 1, 0). VENTURA CO .: 3 miles E Filmore on highway 126 (LBSU 1, 0); 4 miles E Filmore, Santa Clara River wash (LACM 1, 0); 21/2 miles W, 11/2 miles S Simi (LACM 1, 0).

Population 5A.—Los Angeles (68 males, 40 females). CALIFORNIA. LOS ANGELES CO.: 6 miles S, 2 miles E Acton (LBSU 2, 1); Aliso

Canyon (LACM 1, 0); Arroyo Seco, near Pasadena (MVZ 2, 2); Azusa (MVZ 1, 0); San Gabriel River, 3 miles W Azusa (LACM 2, 2); 1 mile SE Big Pine, San Gabriel Mountains, 6,600 feet (KU 2, 0); 6 miles W Big Pines Camp, 5,280 feet (LBSU 1, 0); Burbank (USNM 14, 2); Burbank City Sanitary Landfill (LBSU 0, 1); Chalao Flats (LACM 1, 0); Army Base, Oat Mountain, Chatsworth (LACM 1, 0); base of Oat Mountain, Chatsworth (LACM 0, 1); base S slope Oat Mountain, Brown Canyon, Chatsworth (LACM 1, 0); United States Army Base, Chatsworth (LACM 0, 1); San Gabriel River bottom, near El Monte (MVZ 1, 2); Garnsey, San Fernando Valley (MVZ 2, 1); Glendora (MVZ 0, 1); Horse Flats, San Gabriel Mountains (LACM 2, 2); Horse Flats Campground, San Gabriel Mountains (LACM 1, 1); Little Gleason, 5,700 feet (LACM 1, 0); Little Rock Public Campground, 3½ miles S, 2½ miles W Little Rock (LACM 0, 1); Lopez Canyon (LACM 1, 0); 3½ miles NW Mill Creek Summit (UA 0, 1; LBSU 2, 2); Monrovia (CAS 0, 1); 5 miles S Pearblossom, 4,600 feet (LACM 0, 1); 5 miles S, 0.6 mile E Pearblossom (LACM 3, 0); 4 miles S Pearblossom, 4,600 feet (LACM 0, 1); N side San Gabriel Mountains, Pleasant View Ridge, Juniper Hills, 4,800 feet (UA 4, 2); Pleasant View Ridge, Juniper Hills, 4,800 feet (KU 0, 1); San Fernando (MVZ 2, 0; SDNHM 1, 0); Santiago Canyon, Angeles National Forest (LACM 1, 2); South Fork Camp near Valyermo (LBSU 1, 0); Angeles National Forest, South Fork Camp (LBSU 0, 1); Angeles National Forest, South Fork Camp near Valyermo (LBSU 2, 0); ½ mile N South Fork Camp, Angeles National Forest (LBSU 0, 1); 2 miles S South Fork Public Camp, Angeles National Forest, 4,500 feet (LACM 1, 0); ½ mile S, 2½ miles W Sunland between Glenoaks Boulevard and Hansen Dam (LACM 0, 1); Swartout Valley, Big Pine, 6,900 feet (UCLA 1, 2); mouth of Big Tujunga Canyon (LACM 0, 1); Tujunga Valley (AMNH 1, 0); Tujunga Wash, near San Fernando (MVZ 1, 0); 1/4 mile E Oreas Park, Tujunga Wash (LACM 1, 0); Tujunga Wash, Sunland, 1,400 feet (LACM 1, 0); 5 miles SE Valyermo, San Gabriel Mountains (KU 2, 0); 5 miles SE Valyermo, San Gabriel Mountains, 5,200 feet (KU 1, 0); 10 miles SE Valyermo, San Gabriel Mountains, 5,200 feet (KU 1, 0); 3 miles NE Wrightwood, 3,800 feet (LBSU 1, 0); 3 miles NE Wrightwood on state highway 2, 3,800 feet (LBSU 1, 0); 6.4 miles

W, 4.0 miles N Wrightwood, T4N R8W SW ¼ Sec. 20, Angeles National Forest (MSB 2, 3); 11.2 miles W, 5.1 miles N Wrightwood, T4N R9W SE ¼ Sec. 16 (MSB 1, 0). SAN BERNARDINO CO.: Cajon Pass (USNM 0, 1); Lytle Creek (USNM 0, 1); Lytle Creek Canyon, Applewhite Campgrounds (LBSU 1, 0).

Population 5S.-Los Angeles (29 males, 38 females). CALIFORNIA. LOS ANGELES CO .: Altadena (CAS 2, 3); Arroyo Seco, near Pasadena (MVZ 1, 0); Burbank (USNM 1, 0); Army Base, Oat Mountain, Chatsworth (LACM 0, 1); base S slope Oat Mountain, Brown Canyon, Chatsworth (LACM 0, 1); Covina (UCLA 1, 1); 5 miles E Glendale Civic Center, Scholl Canyon (LBSU 1, 0); 1 mile N, ½ mile W Irwindale City Hall, San Gabriel River bottom (LACM 1, 1); Monrovia (CAS 4, 5); San Fernando (MVZ 3, 2); ½ mile S, 3½ miles W Sunland, 1,060 feet (LACM 1, 1); ½ mile S, 2½ miles W Sunland between Glenoaks Boulevard and Hansen Dam (LACM 0, 2); ½ mile S, 3½ miles W Sunland. Tujunga Wash (LACM 2, 1); 2 miles W, 1/2 mile N Sunland (LACM 7, 3); Tujunga Wash, Sunland, 1,400 feet (LACM 1, 0); ¼ mile N Tujunga Boulevard, Tujunga Wash, Sunland (LACM 0, 1); Tujunga (USNM 1, 0); Tujunga Wash (LACM 0, 1); 4 mile N Foothill Boulevard, Tujunga Wash (LACM 1, 3); 1/4 mile E Oreas Park, Tujunga Wash (LACM 1, 0); ½ mile E Oreas Park, Tujunga Wash (LACM 1, 4). VENTURA CO.: 4 miles E Filmore, Santa Clara River wash (LACM 0, 3); Moore Park College (LACM 0, 1); ½ mile W Moore State College (LACM 0, 1); 4 miles E Moorpark, highway 118, Arroyo Simi (LACM 0, 2); 21/2 miles W, 11/2 miles S Simi (LACM 0, 1).

Population 6A.—Cajon Pass (68 males, 57 females). CALIFORNIA. LOS ANGELES CO .: 4 miles NNE Claremont, 2,000 feet (MVZ 1, 0); mouth San Antonio Canyon, San Gabriel Mountains, 1,900 feet (KU 1, 0). RIVERSIDE CO .: near dam that separates Baustiste Canyon from San Jacinto Valley (LBSU 1, 0); Jurupa Mountains (=7 miles NW Riverside), 1,200 feet (MVZ 1, 0); Jurupa Mountains, 7 miles NW Riverside, 1,200 feet (MVZ 0, 1). SAN BER-NARDINO CO.: 4.4 miles E highway 138 on Arrowhead Road (LBSU 1, 0); 1 mile NE Cajon Pass (LBSU 2, 0); Cajon Wash, 1,100 feet (MVZ 3, 0); Cajon Wash at Devore, 2,200 feet (KU 4, 0); Cajon Wash, ½ mile S Devore (KU 1, 0); Grapelands, mouth Lytle Creek, 1,900 feet (UCLA 2, 2); 2 mile NE Grapeland, 2,000 feet (MVZ 1, 1); 10.0 miles SE Big Bear City, Heart Bar Campground (MSB 2, 2); Heart Bar Campground, San Bernardino National Forest (MSB 1, 0); 8 miles SSE Hesperia (MVZ 0, 1); 14 miles from Hesperia toward lake (MVZ 0, 1); Mojave Camp Site, along deep creek and on rocky hillside (LBSU 1, 0); 2 miles N Muscovy on U.S. 91 (LBSU 1, 0); 11/2 miles NE Ontario. 1,100 feet (MVZ 1, 0); 2 miles ENE Ontario (MVZ 1, 1); 5 miles E Ontario, 1,050 feet (MVZ 1, 1); 7 miles ENE Ontario, 1,050 feet (MVZ 1, 0); 1 mile W on Phelan Road from highway 395 (LBSU 1, 1); Reche Canyon, 1,250 feet (UCLA 1, 2); Reche Canyon, near Colton (LACM 1, 0); Reche Canyon, 4 miles SE Colton, 1,250 feet (MVZ 1, 0); Redlands (MVZ 6, 1); San Timoteo Canyon, 2 miles S Redlands (MVZ 2, 0); San Bernardino (UCLA 0, 1; USNM 2, 0); 3 miles NW San Bernardino, 1,400 feet (UCLA 8, 17); Devils Canyon, 2 miles NW San Bernardino (KU 0, 1); 4 miles NW San Bernardino, 1,500 feet (UCLA 2, 4); 5 miles NW San Bernardino, 1,650 feet (UCLA 1, 0; SDNHM 0, 1); 5 miles NNW San Bernardino, 1,650 feet (UCLA 4, 5); 6 miles N San Bernardino (LBSU 1, 0); 1 mile NW San Bernardino State College, Devil's Canyon (LBSU 1, 0); Sugarloaf, San Bernardino Mountains, 7,500 feet (MVZ 1, 0); 1 mile NE Upland, 1,350 feet (MVZ 3, 1); Deer Canyon Wash, 4½ miles NE Upland (MVZ 1, 0); San Bernardino Mountains, 10 miles S, 13.5 miles E Victorville, 5,200 feet (KU 0, 3); San Bernardino Mountains, 21 miles SE Victorville, 4,500 feet (KU 3, 9); desert slope, San Bernardino Mountains, 21 miles SE Victorville, 5,000 feet (KU 2, 1).

Population 6S.—Cajon Pass (46 males, 38 females). CALIFORNIA RIVERSIDE CO.: 10 miles E Riverside off Reche Canyon Road (LACM 1, 1); 10.4 miles from Barton Road on Reche Canyon Road (LBSU 1, 0); Reche Canyon, 8 miles N, 3 miles W Sunnymead (LBSU 1, 0); 1 mile N Sunnymead (LBSU 0, 1). SAN BERNARDINO CO.: Cajon Wash, 1,100 feet (MVZ 1, 0); 5 miles SE Colton (SDNHM 0, 1); 1 mile W Devore (MSB 1, 0); 1½ miles N, 1 mile E Etiwanda (LBSU 1, 0); Grapelands, mouth Lytle Creek, 1,900 feet (UCLA 1, 3); near Grapelands (SDNHM 1, 0); 2 miles NE Grapeland, 2,000 feet (MVZ 0, 1); Guasti (MVZ 0, 1); Colton (Reche Canyon) (LACM 5, 4); Reche Canyon (MVZ 2, 0); Reche Canyon, 1,250 feet (UCLA 0, 2); Reche Canyon, 5 miles SE Colton (LACM 1, 1); Reche Canyon, 4 miles SE Colton, 1,250 feet (MVZ 9, 5); mouth of Reche Canyon, near Colton, 1,000 feet (MVZ 7, 0); Redlands (MVZ 1, 3); San Timoteo Canyon, 2 miles S Redlands (MVZ 0, 1); San Bernardino (AMNH 1, 0; SDNHM 1, 0; UCLA 0, 2; USNM 2, 0); 3 miles NW San Bernardino, 1,400 feet (UCLA 4, 4); 4 miles NW San Bernardino, 1,500 feet (UCLA 2, 2); 5 miles NW San Bernardino, 1,650 feet (SDNHM 0, 3); 5 miles NNW San Bernardino, 1,650 feet (UCLA 1, 1); 6.4 miles W San Bernardino City, Devore in Lytle Creek Wash, 2,000 feet (LBSU 0, 1); San Timoteo Canyon, 31/2 miles E corner of Barton Avenue and S Timoteo Road (LACM 1, 0); Deer Canyon Wash, 4½ miles NE Upland (MVZ 1, 1).

Population 7S.-Lake Mathews (136 males, 104 females). CALIFORNIA. ORANGE CO.: 5.3 miles E Atwood at end of Esperanza Road (LACM 9, 0; LBSU 1, 0); 5.3 miles E Atwood on Esperanza Road, Rancho Santa Ana (LACM 3, 3; LBSU 1, 1; LSU 1, 1; TCWC 1, 1); Capistrano (USNM 1, 1); 5 miles N, 1 mile E El Toro, 300 feet (LACM 1, 1); Santa Ana Canyon, 400 feet (MVZ 4, 1); Santa Ana Canyon, 1 mile N on Prado Road from Santiago Road (LACM 1, 0); 1 mile W, 1/2 mile N Green River Golf Course, Santa Ana Canyon (LBSU 0, 1); Santa Ana Mountains, Black Star, 1 mile up Black Star Road from Santiago Road (LACM 1, 0); Orange County Disposal Station, Silverado Canyon (LACM 1, 0). RIVERSIDE CO.: 5 miles SW Arlington, 800 feet (LACM 6, 2); Corona (LACM 1, 0); 16 miles E Corona, 2 miles E Temescal Fire Station on highway 71 (LBSU 3, 0); Ortega Highway, El Cariso guard station (LBSU 1, 1); Hemet, San Jacinto Valley (LBSU 0, 1); San Jacinto Valley, 1 mile N Hemet (LBSU 1, 0); San Jacinto Valley, 4 miles E Hemet on road to Idilwild (LBSU 1, 0); 4 miles E Hemet, Remeglio Ranch (LACM 1, 0); 5.3 miles N, 8.8 miles E Hemet, Black Mountain, 5,000 feet (MSB 1, 3); 5.3 miles N, 8.8 miles E Hemet, T4S R2E Sec. 8, Black Mountain, 5,000 feet (MSB 4, 2); 5.3 miles N, 8.8 miles E Hemet T4S R2E SE ¼ Sec. 8, Black Mountain, 5,000 feet (MSB 3, 5); 6.3 miles N, 9.8 miles E Hemet, T4S R2E S ½ Sec. 4 (MSB 1, 1); 7.3 miles N, 9.2 miles E Hemet T4S R2E NW 1/4 Sec. 4 (MSB 0, 3); San Jacinto Valley, 5 miles ENE Lakeview, 1,500 feet (MVZ 3, 3); 3 miles W March Field (LBSU 1, 0); Lake Mathews (LBSU 4, 1); Lake Mathews area (LBSU 1, 0); 1/8 mile SW Lake Mathews (LBSU 1, 1); ¼ mile E Lake Mathews (LBSU 1, 0); Menifee (LACM 3, 0; LSU 2, 2); Menifee, 8 miles S Perris (MVZ 2, 0); 2 miles W Moreno (LACM 1, 1; MVZ 2, 1); S side Mount Russell, 1,850 feet (MVZ 1, 1); SE side Mount Russell, 1,550-1,850 feet (MVZ 1, 2); Murrieta (SDNHM 1, 1); 1 mile NE Murrieta (SDNHM 4, 1); Perris (SDNHM 1, 1); 4 miles E Perris, 1,600 feet (LBSU 2, 0); 4 miles SW Perris (SDNHM 6, 9; UCLA 6, 10); 5 miles SW Perris (MVZ 1, 1); Riverside (FMNH 2, 2); W Riverside (USNM 1, 0); 2 miles S Riverside (KU 1, 1); 7 miles SE Riverside (Schellinger Ranch), 1,600 feet (MVZ 3, 2); 6 miles NW San Jacinto (USNM 1, 0); San Jacinto Lake, 1,000 feet (USNM 1, 0); San Jacinto Valley (USNM 3, 1); 2 miles N Sunnymead (LBSU 1, 0); 3 miles SSE Temecula, 1,025 feet (MVZ 3, 1); Temecula Canyon, 3 miles SW Temecula (LBSU 1, 1); 3 miles SW Temecula, California State Biological Research Station (LBSU 0, 1); Temecula Grade (SDNHM 0, 2); Temecula River (SDNHM 0, 1); Temescal (USNM 1, 0); Santa Ana Mountains, Temescal (USNM 0, 3); Trabuco Canyon, Santa Ana Mountains, 1,500 feet (MVZ 1, 0); 1 1/2 miles W Winchester (LACM 1, 2); 4 miles W Winchester, 1,500-feet (UCLA 21, 23). SAN BERNARDINO CO.: near Lake Mathews (LBSU 1, 1). SAN DIEGO CO.: Elsinore (FMNH 1, 0); 2 miles SE Temecula (LACM 1, 0).

Population 8S.-Cabazon (85 males, 80 females). CALIFORNIA. RIVERSIDE CO.: Badlands, 1 mile E junction highway 60-79, 1,850 feet (MVZ 1, 1); Banning (FMNH 1, 0; USNM 2, 0); Banning, San Jacinto foothills, 2,200 feet (MVZ 2, 0); 1.5 miles SE Banning, 2,100 feet (MVZ 1, 0); 1.5 miles S, 1 mile W Banning, 2,300 feet (MVZ 0, 1); 2 miles E, 0.5 mile S Banning, 2,100 feet (MVZ 2, 2); 21/4 miles WNW Banning, 2,700 feet (MVZ 0, 1); Potrero Canyon, 31/2 miles NE Banning, 2,500 feet (MVZ 1, 0); Banning Canyon, 4,000 feet (LACM 0, 2); foot of Banning Canyon 2,000 feet (LACM 2, 1); Baustiste Canyon, 2 miles E ranger station (LACM 3, 1); Little San Gorgonio Creek, 11/2 miles NW Beaumont, 2,500 feet (MVZ 1, 5); San Timoteo Canyon, 2 miles W Beaumont, 2,400 feet (MVZ 6, 6); 2 miles E, 2 miles S Beaumont, 2,600 feet (MVZ 1, 1); 2 miles E, 3 miles N Beaumont, 3,000 feet (MVZ 0, 2); Lamb Canyon, 3.5 miles SW Beaumont, 2,200 feet (MVZ 4, 4); Potrero Creek, 2 miles E, 5 miles S Beaumont, 2,200 feet (MVZ 1, 1); Cabazon (LACM 11, 11; MVZ 1, 1; SDNHM 11, 17; UCLA 3, 1; UMMZ 5, 1); base of San Jacinto Mountains near Cabazon (MVZ 1, 0); 1/4 mile E Cabazon, 1,800 feet (MVZ 2, 1); 1 mile E Cabazon, 1,700 feet (MVZ 1, 0); 1½ miles S by W Cabazon, 1,700 feet (MVZ 5, 1); 1½ miles W Cabazon, 900 feet (MVZ 4, 5); 1 mile E, 2 miles N Cabazon (LBSU 0, 1); 2 miles W, 1.5 miles N Cabazon, 2,300 feet (MVZ 0, 1); Stubby Canyon, 41/2 miles NE Cabazon, 1,800 feet (MVZ 1, 2); Kenworthy, 4,500 feet, San Jacinto Mountains (MVZ 6, 5); Piñon Flats Campground (LBSU 1, 0); Piñon Flats Public Camp, 4,000 feet (LBSU 1, 0); Schain's Ranch, San Jacinto Mountains, 4,900 feet (MVZ 2, 0). SAN BERNARDINO CO.: 18 miles E Mountain Center, 4,000 feet (MVZ 0, 1); 1 mile S, 1/2 mile E Yucaipa, 2,200 feet (MVZ 2, 3). SAN DIEGO CO.: Schain's Ranch, San Jacinto Mountains, 4,900 feet (LACM 0, 1).

Population 9.-San Luis Rey Valley (151 males, 95 females). CALIFORNIA. SAN DIE-GO CO.: vicinity Bonsall (UMMZ 37, 28); 0.3 mile W, 0.2 mile S Bonsall (UMMZ 2, 1); 34 mile E Bonsall (SDNHM 0, 1); 1 mile S Bonsall (UMMZ 1, 2); 1 mile E Bonsall, 220 feet (SDNHM 0, 1); 1 mile E Bonsall, 350 feet (UMMZ 7, 3); 1.3 miles S, 0.3 mile W Bonsall (SDNHM 15, 4; UMMZ 2, 2); 1.8 miles W, 1.7 miles S Bonsall (SDNHM 1, 0); 2 miles NE Bonsall (LBSU 0, 1); 2 miles E Bonsall (LBSU 2, 0); 3 miles E Bonsall (LBSU 1, 1); 3.6 miles E, 2.0 miles N Bonsall (SDNHM 7, 6); 5 miles NE Bonsall, 270 feet (UCLA 9, 8); 0.2 mile SE Deluz (SDNHM 8, 2); Escondido (CAS 1, 0; KU 6, 5; MVZ 0, 1); 5 miles NE Escondido, 800 feet (UCLA 0, 1); Lake Hodges (SDNHM 1, 0); Orange Glenn (CAS 4, 3); Pala (SDNHM 0, 1); 1 mile S Pala, 500 feet (SDNHM 7, 6; UMMZ 1, 0); 5 miles W Pala (SDNHM 2, 1); Pala Road, 5 miles N Valley Center (SDNHM 1, 1); USMC Reservation, Camp Pendleton (SDNHM 0, 1); 2 miles S Rincon Spring, San Luis Ray River bottom, 1,000 feet (SDNHM 5, 4); San Luis del Rey (FMNH 1, 0); vicinity San Luis Rey Mission (UMMZ 0, 1); 1.3 miles N, 1.3 miles E San Luis Rey Mission, 85 feet (SDSC 2, 0); 1.7 miles N, 1.7 miles E San Luis Rey Mission (SDSC 1, 0); San Pasqual (USNM 0. 1); San Pasqual Valley (FMNH 0, 1; UCLA

1, 0); San Marcos (CAS 14, 3; SDNHM 1, 0); 4 miles N San Marcos (SDNHM 8, 5); Twin Oaks (USNM 3, 0).

Population 10.—Warner Springs (48 males, 32 females). CALIFORNIA. RIVERSIDE CO.: Aguanga (SDNHM 1, 2); 1/4 mile ENE Aguanga, 2,050 feet (MVZ 1, 2); 11/4 miles N, 1/3 mile E Aguanga, 2,300 feet (MVZ 0, 1); 4 miles N Aguanga, Wilson Creek, 2,500 feet (LACM 7, 2); 5 miles E, 3 miles N Aguanga (LACM 3, 3); 6 miles E Aguanga (LACM 1, 0); 1 mile S Dripping Springs (LACM 1, 0); Radec, 2,000 feet (USNM 0, 2); 11 miles SE Temecula at Dripping Springs (LBSU 1, 1). SAN DIEGO CO.: 3 miles SE Aguanga, 2,600 feet (MVZ 3, 0); Banner (MVZ 1, 0; SDNHM 0, 1); Grapevine Springs (MVZ 1, 0); 10 miles N Julien on county road 52 (MVZ 1, 0); 15 miles N Julien on county road 52 (MVZ 1, 0); North Peak, Cuyamaca Mountains (SDNHM 0, 1); Oak Grove (SDNHM 2, 0); Oak Grove Forest Camp (LBSU 3, 2); Mann Ranch, ½ mile NW Oak Grove, 2.800 feet (MVZ 1, 2); Mann Ranch (W side firebreak) ½ mile NW Oak Grove, 2,800 feet (MVZ 2, 0); 2½ miles N Oak Grove (SDNHM 4, 4); 20 miles S Oak Grove Public Camp, take north fork 2 miles E (LBSU 1, 0); Ranchito Road, 2 miles E of San Diego highway 2 (LBSU 1, 0); 2 miles E San Diego 2 on road to Ranchito (LBSU 2, 2); Santa Ysabel (AMNH 2, 2; FMNH 1, 0; LBSU 0, 2); Scissors Crossing, Earthquake Valley (MVZ 0, 1); 2 miles E on San Diego 2 from North Scissors (LBSU 1, 0); Silverent Palomar Mountain (SDNHM 0, 1); Sourdough Spring, T10S R1E, Cleveland National Forest, 6,140 feet (MSB 3, 0); 1 mile W Warner's Hot Springs (SDNHM 1, 0); 6.7 miles NW Warner Springs, Cleveland National Forest (MSB 2, 1).

Population 11.—San Diego (99 males, 70 females). BAJA CALIFORNIA. North side Descanso Bay (SDNHM 1, 0); 5 miles S Monument 258, westcoast (MVZ 0, 1); Rosarito (FMNH 2, 3); Rosarito Beach (SDNHM 0, 1); Rosarito Divide (FMNH 1, 0); Tijuana (USNM 0, 1); Valle de las Palmas (MVZ 1, 0; SDNHM 4, 1); S end Valle de las Palmas, 1,200 feet (MVZ 4, 1). CALIFORNIA. SAN DIEGO CO.: Bonita (SDNHM 2, 0); 2 miles SE Bonita (SDNHM 0, 1); Camp Elliot Naval Reservation (SDNHM 1, 0); Camp Elliot Naval Reservation, 575 feet (SDNHM 1, 0); Camp Elliot, 5.75 miles S, 2.2 miles W Poway Post Office (SDNHM 1, 0); ¼ mile S Camp Minnewawa, 650 feet (SDSC 1,

0); 14 miles S, 4 mile E Camp Minnewawa, 1,950 feet (SDSC 1, 0); Chula Vista (MVZ 2, 0); S slope Cowles Mountain (SDNHM 0, 1); Del Mar (LACM 1, 1); 1¾ miles S, 1¾ miles E Del Mar (LACM 0, 2); Dulzura (CAS 0, 1; LACM 14, 10; MVZ 2, 0; SDNHM 4, 11; UCLA 10, 11; UMMZ 1, 0; USNM 2, 4); 3 miles E Dulzura (SDNHM 3, 0); Hillsdale (SDNHM 3, 1); Hillsdale, vicinity of El Cajon (UCLA 0, 1); Murphy Canyon (AMNH 1, 0; SDNHM 1, 0); San Diego (AMNH 9, 5; SDNHM 1, 2; UCLA 2, 1; USNM 2, 0); East San Diego (SDNHM 2, 0); East San Diego, Hummingbird Canyon (SDNHM 0, 1); Jamul (FMNH 1, 0); Jamul Creek near El Mido (USNM 1, 0); near Rancho Santa Fe (UI 0, 1); Rose Cañon (USNM 1, 0); Mission Bay, San Diego (SDNHM 1, 0); San Diego River Gorge (SDNHM 1, 0); ½ mile N State College (SDSC 0, 1); Suncrest (MVZ 1, 0; SDSC 1, 0); 2 miles N Sweetwater Dam (MVZ 2, 1); Tijuana River, near Monument 258 (SDNHM 1, 0); near mouth Tijuana River (MVZ 8, 3; SDNHM 0, 1); vicinity of the mouth of the Tijuana River (UCLA 1, 0); United States-Mexico Boundary, ½ mile NE Monument 257, 350 feet (UCLA 0, 2).

Population 12.-Jacumba (51 males, 38 females). BAJA CALIFORNIA. 1 mile S El Condor, km 2895 (LBSU 1, 2); side of Jacumba (UI 1, 1); S of Jacumba Airport, Jacumba (UI 1, 0); International Boundary at Jacumba (SDNHM 5, 3); 3 miles NW Neji (SDNHM 1, 0); 13 miles W, 1 mile N Rumorosa (MVZ 1, 1). CALIFOR-NIA. SAN DIEGO CO.: 1/2 mile W Boulevard, 3,500 feet (UCLA 1, 4); Campo, 2,180 feet (UCLA 6, 1); Jacumba (MVZ 3, 4; UCLA 13, 6); S of Jacumba Airport (UA 1, 0); ¼ mile S Jacumba (MVZ 0, 1); 1 mile S Jacumba (MVZ 1, 0); 11/4 miles E Jacumba, 2,900 feet (UCLA 6, 6); 2 miles E Jacumba, 3,000 feet (UCLA 3, 1); 21/2 miles W Jacumba on highway 94 (LBSU 2, 0); 3 miles E Jacumba on flat plain near base of mountains, 3,200 feet (LBSU 0, 1); 31/4 miles N Manzanita, McCain Valley, 3,600 feet (MVZ 1, 4); ¼ mile S Mountain Spring, 3,300 feet (UCLA 2, 1); 2 miles W Live Oak Springs, 3,400 feet (UCLA 1, 1); Pine Valley (SDNHM 1, 0); Sunrise Highway, Laguna Mountains (SDNHM 0, 1).

Population 13.—Ensenada (47 males, 41 females). BAJA CALIFORNIA. 10 miles SE Alamo (SDNHM 13, 19); Ensenada (FMNH 3, 4; SDNHM 0, 1; USNM 4, 1); 12 miles N Ensen-

ada (MVZ 1, 0); 14 miles S Ensenada (SDNHM 1, 0); Punta Banda (LBSU 8, 6); Punta Banda, 20 miles SW Ensenada (LBSU 1, 1); San Jose (SDNHM 3, 2); Santo Tomas (MVZ 1, 0; SDNHM 5, 3); San Tomas (FMNH 4, 1); 15 miles S San Tomas, Mexico highway 1 (LBSU 0, 1); San Vincente (UMMZ 0, 1); 4 miles S San Vincente (UMMZ 0, 1); 10 miles SW San Vicente (LBSU 1, 0); 38 miles S Tecate at El Chapo Mines, 3,600 feet (AMNH 2, 0).

Population 14.-Sierra Juarez (62 males, 54 females). BAJA CALIFORNIA. Rancho Viejo, 15 miles E Alamos (USNM 4, 1); Aqua Hechicera 32°30'N 116°16'W (MVZ 4, 3); El Rayo, Sierra Juarez (SDNHM 4, 5); 4 miles S El Topo (LBSU 0, 1); La Heurta, W base Laguna Hanson Mountains (USNM 2, 0); Laguna Hanson (MSB 1, 0); Laguna Hanson, Sierra Juarez (SDNHM 5, 7; MVZ 2, 3; MSB 1, 1); 14 miles N Laguna Hanson, Sierra Juarez, 6,000 feet (CAS 6, 2); Los Pozos, Sierra Juarez, 4,200 feet (MVZ 3, 2); Ojos Negros (SDNHM 1, 5); Rancho Ojos Negros, 2,200 feet (MVZ 4, 3); 3 miles E Ojos Negros (SDNHM 20, 14); Sangre de Cristo (SDNHM 5, 4); Tres Piños Mine near Juarez (SDNHM 0, 3).

Population 15.-Valle de Trinidad (145 males, 157 females). BAJA CALIFORNIA. Mike's Sky Rancho (MSB 1, 1); Mike's Sky Rancho, Sierra San Pedro Martir (MSB 1, 0); Arroyo San Pedro Martir, Mike's Sky Rancho, 10.9 miles E, 20 miles S Valle de Trinidad (MSB 1, 2); El Alamo (FMNH 0, 2); El Valle de la Trinidad, 2,500 feet (MVZ 7, 7); Valle de Trinidad (UOMZ 9, 13); Valle de la Trinidad (SDNHM 24, 28); Valle de la Trinidad, at extreme W end (SDNHM 5, 6); west end Valle de Trinidad (UOMZ 1, 0); 4 miles S Valle de Trinidad (UOMZ 10, 15); Valle de la Trinidad, Aguajito Spring (SDNHM 55, 67); Valle de la Trinidad, Colonia San Cardenas (LBSU 0, 1); 8 miles S, 9 miles E Valle de Trinidad (MSB 2, 4); 16 miles S, 5 miles E Valle de Trinidad (MSB 2, 2); 16 miles S, 5 miles E Valle de Trinidad, San Pedro Martir (MSB 1, 0); San Lazard Cardenas (Campbell's Ranch) (LBSU 2, 1); 19.9 miles E San Telmo (MSB 2, 0); Trinidad (FMNH 1, 1); La Zapopita, Valle Trinidad (LACM 5, 4); ¼ mile N La Zapopita, Valle Trinidad (LACM 16, 3).

Population 16.—San Quintin Plain (65 males, 51 females). BAJA CALIFORNIA. Agua Chiquita Canyon (SDNHM 4, 1); Aguaje del Sauce,

2,600 feet (MVZ 0, 4); Colnett, latitude 31°N (MVZ 0, 1); Colonia Guerrero (LACM 2, 0); 2 miles E Colonia Guerrero (UOMZ 1, 0); 3 km SW Colonia Guerrero (MSB 1, 0); Las Cabras (SDNHM 1, 1); San Antonio Ranch, Santo Domingo River, 2,100 feet (MVZ 1, 1); San Jose, latitude 31°N, 2,500 feet (MVZ 5, 3; UCLA 0, 2); San Quintin (FMNH 2, 1; MVZ 2, 0; SDNHM 8, 3; USNM 0, 1); near San Quintin (SDNHM 0, 1); north end of San Quintin Plain (SDNHM 0, 1); near rock bluff, 8 miles N San Quintin (SDNHM 1, 0); 8.5 miles N San Quintin (UOMZ 1, 1); 10 miles E San Quintin (SDNHM 2, 2); NE side San Quintin Bay (SDNHM 1, 0); 1 mile S San Ramon (SDNHM 1, 0); San Telmo (MVZ 6, 12); Santo Domingo (LACM 1, 0; MVZ 3, 2; SDNHM 16, 11; USNM 1, 0); Socorro, 20 miles S San Quintin (MVZ 2, 0); Valladares, 2,700 feet (AMNH 1, 0; MVZ 2, 3).

Population 17.—San Pedro Martir (31 males, 23 females). BAJA CALIFORNIA. Concepcion, Sierra San Pedro Martir, 6,000 feet (MVZ 1, 1); La Grulla Sierra San Pedro Martir (MVZ 2, 2; SDNHM 2, 0); Piñon, W slope San Pedro Martir Mountains (USNM 1, 3); head San Antonio River (FMNH 1, 2); Santa Eulalia, San Pedro Martir Mountains (FMNH 2, 2); Summit San Martir Pass, Diabbito Spring (SDNHM 17, 8); Summit San Martir near Diabbito Spring (SDNHM 5, 5).

Population 18.—El Rosario (41 males, 35 females). BAJA CALIFORNIA. Ajuaita (El Aguajito) (SDNHM 2, 1); mouth Canyon San Juan de Dios (SDNHM 8, 7); Rosario (UCLA 14, 9); 1 mile E El Rosario (MVZ 1, 2; SDNHM 4, 0); 4 miles E El Rosario (SDNHM 1, 5); 6 miles N El Rosario (LBSU 1, 1); 6 miles E El Rosario (LACM 2, 0; UOMZ 2, 4); 8 miles N El Rosario (MVZ 1, 0); 10 miles E El Rosario (SDNHM 1, 3); 12 miles N El Rosario (UOMZ 2, 2); 12 miles E El Rosario (LBSU 1, 1); 20 miles E El Rosario (MVZ 1, 0).

Population 19.—San Agustin (64 males, 37 females). BAJA CALIFORNIA. 10 miles S El Marmol (CAS 0, 2); 12.5 miles by road S El Marmol, 2,200 feet (MVZ 1, 4); 13 miles SW El Marmol (LBSU 2, 0); Rancho Ramona, 13 miles SW San Agustin (SDNHM 5, 0); Rancho La Ramona 8 miles N Santa Catarina (SDNHM 4, 4); San Agustin (MVZ 2, 0; SDNHM 10, 5; UOMZ 19, 13); San Fernando, 1,100 feet (MVZ 7, 2); San Fernando Mission (SDNHM 2, 0); 5 miles SE San Fernando (SDNHM 5, 2); 20 miles E San Fernando, Pozo San Augustine (USNM

0, 1); 7 miles N Santa Catarina (SDNHM 2, 2); 8 miles N Santa Catarina (SDNHM 5, 2).

Population 20.—Santa Catarina (19 males, 25 females). BAJA CALIFORNIA. Rancho Santa Catarina (MSB 1, 6); 34 miles SW San Agustin in Santa Catarina Mountains (LBSU 2, 4); Santa Catarina Landing (MSB 4, 3; SDNHM 4, 7; UOMZ 7, 3); 4 miles N Santa Catarina Landing (SDNHM 0, 2; UOMZ 1, 0).

Population 21.—Laguna Chapala (38 males, 34 females). BAJA CALIFORNIA. Catavina, 1,850 feet (MVZ 7, 4); 2 miles N Catavina (SDNHM 2, 0); 7 miles S Catavina (SDNHM 0, 3); 2 miles NW Chapala (SDNHM 21, 17); 13 miles NW Chapala (SDNHM 6, 4); Laguna Seca Chapala (MVZ 1, 2); 24 miles NW Punta Prieta, 2,000 feet (MVZ 0, 1); 25 miles N Punta Prieta (SDNHM 0, 3); 55 miles N Punta Prieta, 2,500 feet (MVZ 1, 0).

Population 22.—San Andres (45 males, 26 females). BAJA CALIFORNIA. Agua Amarga (SDNHM 4, 0); 8 miles SE El Rosarito (LBSU 0, 2); Punta Prieta (CAS 1, 1; SDNHM 15, 7); 11 miles S Punta Prieta (SDNHM 1, 0); 2 miles NE Rosarito (MSB 4, 1); San Andres (SDNHM 1, 1; USNM 1, 1); Mission de San Borjas (MSB 4, 1; SDNHM 2, 4; UOMZ 8, 5); San Juan Mine, Sierra San Borjar, 4,000 feet, 28°50'N (SDNHM 4, 2); Valle de Agua Amarga, 15 miles W Bahia Los Angeles (SDNHM 0, 1).

Population 23.-Mesquital (68 males, 60 females). BAJA CALIFORNIA. Calmalli (MVZ 1, 0; SDNHM 5, 7); 15 miles E Calmalli, Rancho Union (SDNHM 2, 1); 1 mile E El Arco (SDNHM 0, 4); 4 miles E El Arco (SDNHM 3, 1); 12 miles E El Arco (SDNHM 3, 5); 5 miles W El Cañon (SDNHM 3, 1); 1 mile E Rancho Lajunitas (SDNHM 2, 0); 1 mile E Rancho Lajunitas, 28°30'N (SDNHM 0, 1); 2.5 miles W Mesquital (UOMZ 18, 17); 10 miles SE Mesquital, 400 feet (MVZ 13, 12); 10 miles S Rancho Mesquital (MVZ 0, 1); 7 miles W San Francisquito Bay (SDNHM 9, 5; UOMZ 2, 0); Santo Domingo (USNM 3, 1); Santo Domingo Landing, 28°15'N (SDNHM 3, 3); Santa Gertrudis Mission (SDNHM 1, 1).

Population 24.—San Ignacio (33 males, 31 females). BAJA CALIFORNIA SUR. 15 miles S El Arco (LBSU 1, 0); Campo Los Angeles (SDNHM 3, 6); Mesquital (SDNHM 9, 6); 13 miles E Ojo de Liebre, Viscaino Desert, 100 feet (LACM 1, 0); San Ignacio, 500 feet (MVZ 2, 3; SDNHM 2, 1; USNM 2, 1); 10 miles E San

Ignacio (UOMZ 11, 9); La Esperanza Rancho, 12 miles E San Ignacio, 900 feet (MVZ 0, 1); 18 miles E San Ignacio (SDNHM 0, 1); 2 miles SE Rancho los Martiles (=23 miles W San Ignacio), 150 feet (LACM 1, 1); 10 miles W Santa Rosalia (SDNHM 1, 1); 10 miles W Santa Rosalia, Valle de Yagin, 28°15′N (SDNHM 0, 1).

Population 25.—Magdalena Plain (33 males, 37 females). BAJA CALIFORNIA SUR. 4.5 miles N El Refugio (UOMZ 24, 19); 7 miles N El Refugio (SDNHM 0, 1); 9 miles S El Refugio (SDNHM 2, 2); 24.3 miles SE El Refugio, 100 feet, 24°33′N 111°35′W (MVZ 3, 5); W end Llano de Hirey, 50 feet (MVZ 0, 1); Matancita, 100 feet (MVZ 1, 1; USNM 1, 0); San Jorge, 25°44′N 112°07′W (MVZ 0, 1; SDNHM 0, 1); Santo Domingo, 25°31′N (SDNHM 2, 6).

Dipodomys stephensi (36 males, 26 females).—CALIFORNIA. KERN CO.: Last Chance canyon, 2½ miles N, 2 miles W Saltdale (LAMC 0, 2). RIVERSIDE CO.: ½ mile S Eden Hot Springs, 1,500 feet (MVZ 0, 1); 3 miles N, 2 miles W Sunnymead (UMMZ 0, 1); 4 miles SW Perris (SDNHM 8, 4); 5.1 miles NM Santa Rosa Ranch House, Santa Rosa Ranch, Santa

Ana Mountains, 2,100 feet (LAMC 5, 4); Badlands, T3S, R2W, SW 1/4 SE 1/4 Sec. 10, SBBM, 1,800 feet (LACM 0, 1); Elsinore, T5S, R4W, NW ¼ Sec. 20 SBBM, 1,600 feet (LACM 0, 1); Good Hope Mine (KU 1, 0); Good Hope Mine, 5 miles SW Perris (MVZ 3, 2); Perris, T4S, R4W, SE ¼ NW ¼ Sec. SBBM, 2,000 feet (LAMC 1, 0); Perris Valley, T5S, R3W, SE 1/4 SE 1/4 Sec 18, SBBM, 1,500 feet (LAMC 1, 1); Railroad Canyon, T5S, R4W, NE 1/4 Sec. 33, SBBM, 1,600 feet (LAMC 2, 0); Railroad Canyon, T5S, R4W, NE ¼ SE ¼ Sec. 34 SBBM, 1,400 feet (LAMC 0, 1); Riverside (FMNH 1, 1); Steele Peak, T5S, R4W, NE 4 SW 4, Sec. 9 SBBM, 2,000 feet (LAMC 2, 0); Winchester, T6S, R2W, NE ¼ NE ¼ Sec. 6, SBBM, 1,500 feet (LAMC 1, 1). SAN BERNARDINO CO .: Reche Canyon, 4 miles SE Colton, 1,250 feet (MVZ 1, 0). SAN DIEGO CO.: 1 mile E Bonsall (SDNHM 4, 5); 2 miles E, 0.6 mile S San Luis Rey Mission (SDNHM 4, 1); 7.1 miles E Oceanside (SDNHM 1, 0); Fallbrook Naval Weapons Station, 8 miles EEN South Gate Guard Station and 1.5 miles W of E Perimeter Road, 775 feet (LAMC 1, 0).