Kangaroo Rats: Intraspecific Variation in *Dipodomys spectabilis* Merriam and *Dipodomys deserti* Stephens

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ABSTRACT

Twenty morphological characters in addition to color were studied throughout the geographic range of two species of kangaroo rats, the banner-tailed kangaroo rat *Dipodomys spectabilis* and the desert kangaroo rat *Dipodomys deserti*. A total of 2,725 specimens from 689 localities was examined in this study: 1,187 specimens from 368 localities for *D. spectabilis* and 1,538 specimens from 321 localities for *D. deserti*. The two species are characterized and notes are given concerning their habitat, longevity, predators, parasites, molt, and reproductive activity. There seems to be one adult molt per year in each of the two species. This takes place during every month, but mostly in August for *D. spectabilis* and in July for *D. deserti*. Color of the pelage is more stable in *D. spectabilis* and is less influenced by environmental factors than in *D. deserti*.

None of the characters studied shows significant secondary sexual dimorphism in *D. spectabilis*, whereas nine characters show significant dimorphism in *D. deserti*. The level of differentiation among the subspecies of *D. spectabilis* is higher than that of *D. deserti*. This difference is thought to be the result of a longer period of isolation of some of the populations of *D. spectabilis* and of the availability of more varied habitat within the range of this species. The low degree of variability throughout the range of *D. deserti* is probably due to the uniformity of the habitat, the absence of effective geographic barriers, and to the species' narrow limits of tolerance. Some of the measurements of *D. deserti* show southward clinal changes. Nasal length and rostral depth increase in size in this direction, and this is thought to be directly correlated with an increase in temperature and a decrease in humidity of the environment.

Seven subspecies of *D. spectabilis* and four subspecies of *D. deserti* are recognized and are formally diagnosed. *D. nelsoni*, which was formerly regarded as a full species, is regarded herein as a subspecies of *D. spectabilis*. *D. s. clarencei* is regarded as consubspecific with *D. s. baileyi*.

A brief review of the fossil history of the genus *Dipodomys* is given. It is assumed that *D. spectabilis* originated in the northern part of the

Central Plateau of Mexico and *D. deserti* in southeastern California. A pattern of dispersal for each of these two species is proposed.

Four indices of specialization (bullar, cranial, pedal, and total) were calculated for each subspecies of the two species. Within *D. spectabilis*, the most specialized subspecies is *D. s. nelsoni*, and within *D. deserti*, the most specialized is *D. d. deserti*. Also the data from the indices have led to the conclusion that *D. deserti* is more specialized than *D. spectabilis* in all the indices calculated, and that it is phylogenetically far removed from it. Also, it is concluded that *D. deserti* is the most specialized species of the genus *Dipodomys* and therefore should be retained in a separate *deserti* Group.

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INTRODUCTION

For a better understanding of the evolutionary processes that have occurred and are occurring in a species, the infraspecific units should be identified and the relationships among them analyzed. To achieve these aims, the variation of significant characters throughout the entire geographic range of the species must be studied and correlated to analyze the whole. Variation within two species of kangaroo rats, *Dipodomys spectabilis* and *Dipodomys deserti*, has been so analyzed and life-history data added.

Dipodomys spectabilis was described by C. H. Merriam in 1890 from specimens obtained at Dos Cabezas, Cochise County, Arizona, and *Dipodomys deserti* by F. Stephens in 1887 from specimens from the Mojave River, San Bernardino County, California. Since the original descriptions, no further study of geographic variation throughout the entire range has been conducted in either species. Although they approach each other geographically in south central Arizona, the species are allopatric. Both have been collected near Florence, Pinal County, and also within Organ Pipe Cactus National Monument, Pima County.

Dipodomys, the only living genus of the subfamily Dipodomyinae, is one of three subfamilies of the family Heteromyidae. Grinnell's (1922) study of the kangaroo rats of California was the closest attempt to a revision of the genus *Dipodomys*. Since then, Hall and Dale (1939) revised *D. microps*; Setzer (1949) *D. ordii*; Lidicker (1960) *D. merriami*, and Alvarez (1960) wrote a synopsis of the Mexican species of *Dipodomys*. The present paper is a revision of data pertaining to the banner-tailed kangaroo rat *Dipodomys spectabilis* and the desert kangaroo rat *Dipodomys deserti*.

The phylogenetic relationship between *D. spectabilis* and *D. deserti* has been discussed by a number of authors using a variety of evidences (Grinnell, 1922; Setzer, 1949; Burt, 1960; Lidicker, 1960; Stock, 1974). Some of the authors showed the close relationship between the two

species and placed them in one phylogenetic group, while other investigators placed them in two separate groups. Nevertheless, most of these authors agreed that *D. deserti* is the most specialized species in the genus *Dipodomys*. The present study discusses the relationship between the two species and arrives at similar conclusions.

MATERIALS AND METHODS

This study is based on the examination of 1,187 specimens of *Dipodomys spectabilis* from 368 localities and of 1,538 specimens of *Dipodomys deserti* from 321 localities for a total of 2,725 specimens from 689 localities. Notes were taken on the color of the pelage for all specimens. For both species comparisons of color were made with the type-specimen, topotypes, or other specimens previously compared with topotypes. The notes include information on the color of the dorsum, arietiform markings, plantar stripes, dorsal and ventral tail stripes, and the subterminal band of the tail. Capitalized color terms are from Ridgway (1912). To determine the color, a masked area of pure color on the side just above the lateral line was compared with a certain color on Ridgway's plates in daylight always from the same angle.

All information available on the specimen label was utilized. Body length was calculated as the difference between the total length and tail length. Length of the white tip of the tail was measured to the nearest millimeter, from the base of the proximal part of the white tail tip to the approximated tip of the tail vertebrae in the study specimen. For all the specimens the following 14 measurements of the skull were taken with the same pair of dial calipers (Helios), measuring to 0.1 mm and read to the nearest 0.1 mm (Fig. 1):

Greatest length. From the anteriormost tip of the nasals to the posteriormost projection of the auditory bullae.

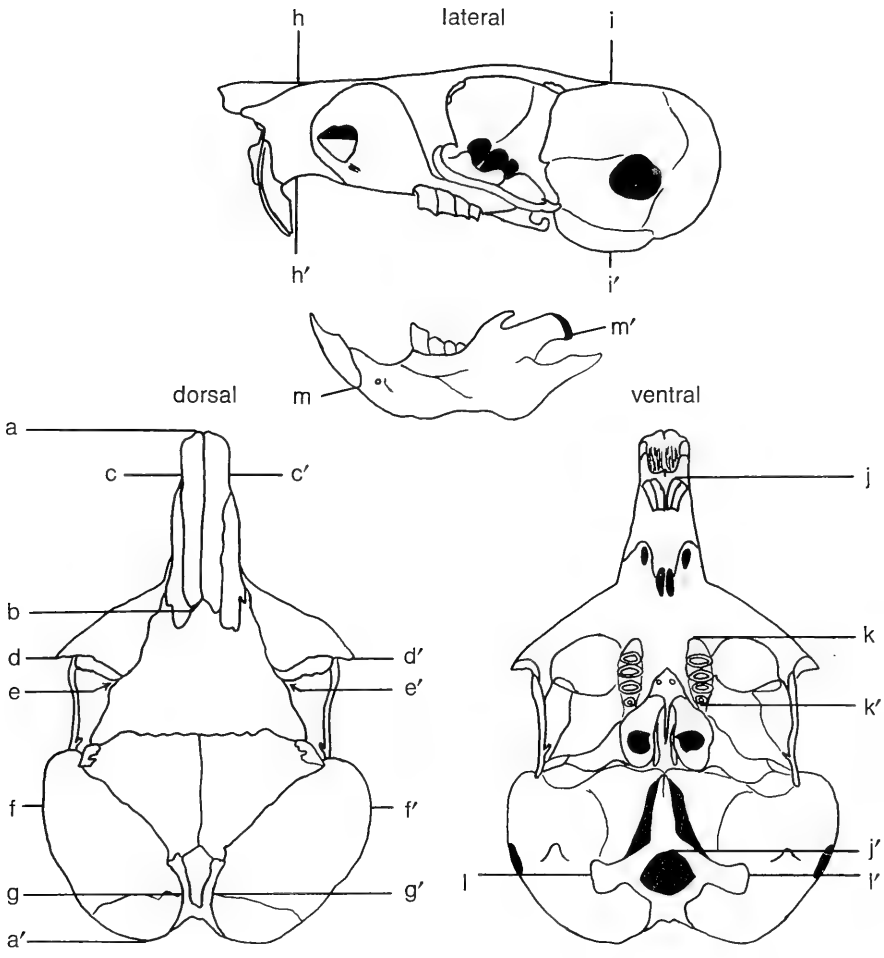
Length of nasals. Maximum length of the longest nasal bone.

Breadth of rostrum. Width near the anterior tip of the rostrum, across the premaxillae and nasals at the anterior face of the upper incisors.

Breadth across maxillary arches. Greatest breadth across the arches in a plane perpendicular to the long axis of the skull.

Least interorbital breadth. Least width between the orbits immediately posterior to the lacrimal bones.

Greatest breadth across bullae. From the most lateral projection of



a, a′	greatest skull length	h, h′	depth of rostrum
a, b	length of nasals	i, i′	bullar depth
c, c′	width of rostrum	j, j′	basal length
d, d′	breadth across maxillary arches	k, k′	alveolar length of maxillary toothrow
e, e′	least interorbital breadth		
f, f′	greatest breadth across bullae	l, l′	breadth across exoccipitals
g, g′	least width of supraoccipital	m, m′	mandibular length

Fig. 1. *Dipodomys spectabilis perblandus*, UI No. 14808 ♂, 7 mi NW Nogales, Santa Cruz County, Arizona. Dorsal, ventral, and lateral views showing skull measurements used in this study.

the auditory bullae on one side to the corresponding position on the other bulla.

Least supraoccipital breadth. Width at narrowest part.

Depth of rostrum. Depth of the premaxillae and the nasals taken immediately posterior to the upper incisors.

Bullar depth. Greatest depth measured at a right angle to the long axis from across the dorsal surface of the skull to the most ventral surface of the bullae.

Basal length. From the anterior border of the alveolar ridge anterior to the upper incisors to the anterior border of the foramen magnum, ventrally.

Alveolar length of maxillary toothrow. Greatest distance from the anterior edge of the alveolus of PM4 to the posterior edge of the alveolus of M3.

Breadth across exoccipitals. Greatest distance from the lateral edge of the exoccipital on one side to the corresponding edge on the other side.

Alveolar length of mandibular toothrow. From the anterior edge of the alveolus of pm4 to the posterior edge of the alveolus of m3.

Mandibular length (Condyloid). Distance between the anterior lower lip of the incisive alveolus and the posteriormost border of the condyloid process.

Little use was made of ear measurement, as it was not available for a large number of the specimens examined, and measurements of dry ears proved to be unsatisfactory. The least supraoccipital breadth and the length of the white tip of the tail were not utilized for *D. deserti* because these dimensions proved to be highly variable. The coefficients of variation for 16 males and 13 females from the vicinity of Yuma, Yuma County, Arizona, for the least supraoccipital breadth were 124.92 and 83.15, respectively. The coefficients of variation for 18 males and 13 females from the same locality for the length of the white tip of the tail were 48.34 and 30.12, respectively.

In analyzing differences among age groups and in analyzing the secondary sexual dimorphism, standard deviation and standard error of the mean were calculated for each measurement. Comparisons of the means were made following the method outlined by Mayr, Linsley, and Usinger (1953:142).

The age of each specimen was determined. Five age-groups are recognized in *D. spectabilis*: juvenile, immature, subadult, young adult, and old adult. Since no significant differences were found between the

young adult and the old adult age-groups, they were subsequently combined and called adults (see Age Variation, p. 16). In *D. deserti* only four age-groups were recognized: juvenile, immature, subadult, and adult. Only adults were used for taxonomic and statistical purposes.

Adult males and females were compared, and the differences between the means in *D. spectabilis* were not statistically significant (see Secondary Sexual Dimorphism under *D. spectabilis,* p. 22). Thus, data for the two sexes were combined when the measurements were plotted on the working maps. The differences between the means in *D. deserti* were statistically significant in some measurements (see Secondary Sexual Dimorphism under *D. deserti,* p. 77) and, accordingly, these measurements were plotted separately on the working maps.

Some localities close to each other were grouped in order to obtain larger samples; nevertheless, distance and physiographic features were taken into consideration.

T-tests were made for certain localities and scatter diagrams were often used in comparing different populations.

Indices used to determine the degree of specialization of each subspecies of *D. spectabilis* and *D. deserti* and of each species as a whole were the following (after Lidicker, 1960:129):

Bullar Index: greatest breadth across the bullae/breadth across the maxillary arches.

Cranial Index: greatest breadth across the bullae/greatest length of the skull.

Pedal Index: length of hind foot/body length.

Index of Total Specialization: An average of the three indices combined (bullar, cranial, and pedal) $\times$ 100.

The average for each character at each locality, or group of localities, was plotted on a map on tracing paper, and lines were drawn whenever an appreciable break or shift in the character was noticed. All maps were combined in order to determine the subspecific boundaries where the largest number of lines fell together.

In the account of subspecies, the synonomy consists of all the names which have been used for the subspecies recognized in this study. Pertinent information about the type-specimen of each recognized subspecies is included within the account of that subspecies under *Type.* Name combinations recorded in literature for the first time are also included in the synonomy. Under *Specimens examined,* states are listed in order of occurrence from north to south and from west to east. Counties in each state and localities within the counties follow the

same arrangement. *Additional records* include specimens known but not examined by me.

The following abbreviations are used throughout this report in referring to the different collections.

AMNH	American Museum of Natural History, New York, New York
ASU	Arizona State University, Tempe, Arizona
CAS	California Academy of Science, San Francisco, California
CM	Carnegie Museum, Pittsburg, Pennsylvania
DGC	Dirección General de Caza de la Secretaria de Agricultura y Ganaderia, México
FMNH	Field Museum of Natural History, Chicago, Illinois
KU	Museum of Natural History, University of Kansas, Lawrence, Kansas
LACM	Los Angeles County Museum, Los Angeles, California, including the Allan Hancock Collection
LSU	Louisiana State University, Museum of Zoology, Baton Rouge, Louisiana
MSU	The Museum, Michigan State University, East Lansing, Michigan
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California
NMSUWC	New Mexico State University, Wildlife Collection, University Park, New Mexico
SDSNH	San Diego Society of Natural History, San Diego, California
SRSC	Sul Ross State College, Alpine, Texas
TCWC	Texas A&M University, Cooperative Wildlife Collection, College Station, Texas
TMM	Texas Memorial Museum, Natural History Collection, Austin, Texas
UA	Department of Zoology, University of Arizona, Tucson, Arizona
UCLA	University of California at Los Angeles, Los Angeles, California, including the Donald R. Dickey Collection
UI	Museum of Natural History, University of Illinois, Urbana, Illinois
UM	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
UNM	University of New Mexico, Collection of Vertebrates, Albuquerque, New Mexico

USNM United States National Museum and Biological Surveys Collection, Washington, D.C.

UU Museum of Zoology, University of Utah, Salt Lake City, Utah

DIPODOMYS SPECTABILIS

Species Characteristics

The banner-tailed kangaroo rat, with an adult weight range from 77.0 to 171.2 grams, is one of the largest species of the genus *Dipodomys*. It has four toes on the hind foot. The hind legs and feet are larger and much longer than the fore legs, an adaptation for saltatorial locomotion. The tail is long, covered with short hairs on the proximal half and with long hairs on the distal half. The color of the dorsum, in general, is Light Ochraceous-Buff, mixed with a variable growth of black-tipped hairs, purest on the sides and lightest on the cheeks. The supraorbital and postauricular spots, hip stripes, fore limbs, dorsal surface and sides of hind feet, lateral tail stripes, ventral surface, and the distal end of the tail are pure white. The Ochraceous hip patch extends down the leg behind the ankle to form a large dark spot that reaches the heel and leaves a white spot anteriorly. The white ring at the base of the tail is incomplete, with gray to black colored hairs ventrally. The dorsal and ventral tail stripes, which are grayish black to dusky, unite to form a continuous black or almost black band around the tail subterminally. The white lateral tail stripes narrow gradually beyond the proximal half of the tail and disappear at the subterminal band.

The skull is large, with inflated bullae. The interparietal bone is variable in size and shape and sometimes fused with the supraoccipital. The maxillary arches are heavy and their posterolateral edges are slightly slanted or flared out. The dorsal anteromedial edge of the maxillary arch is narrow and extends slightly along the premaxilla. The teeth are medium to massive in size and the molariform teeth are of the opaeodont type (Nader, 1966). The upper incisors are grooved anteriorly. A depression, here called the "ectoglenoid fossa," for the attachment of the ventral slip of the temporal muscle is present between the glenoid fossa and the posterior end of the zygomatic arch.

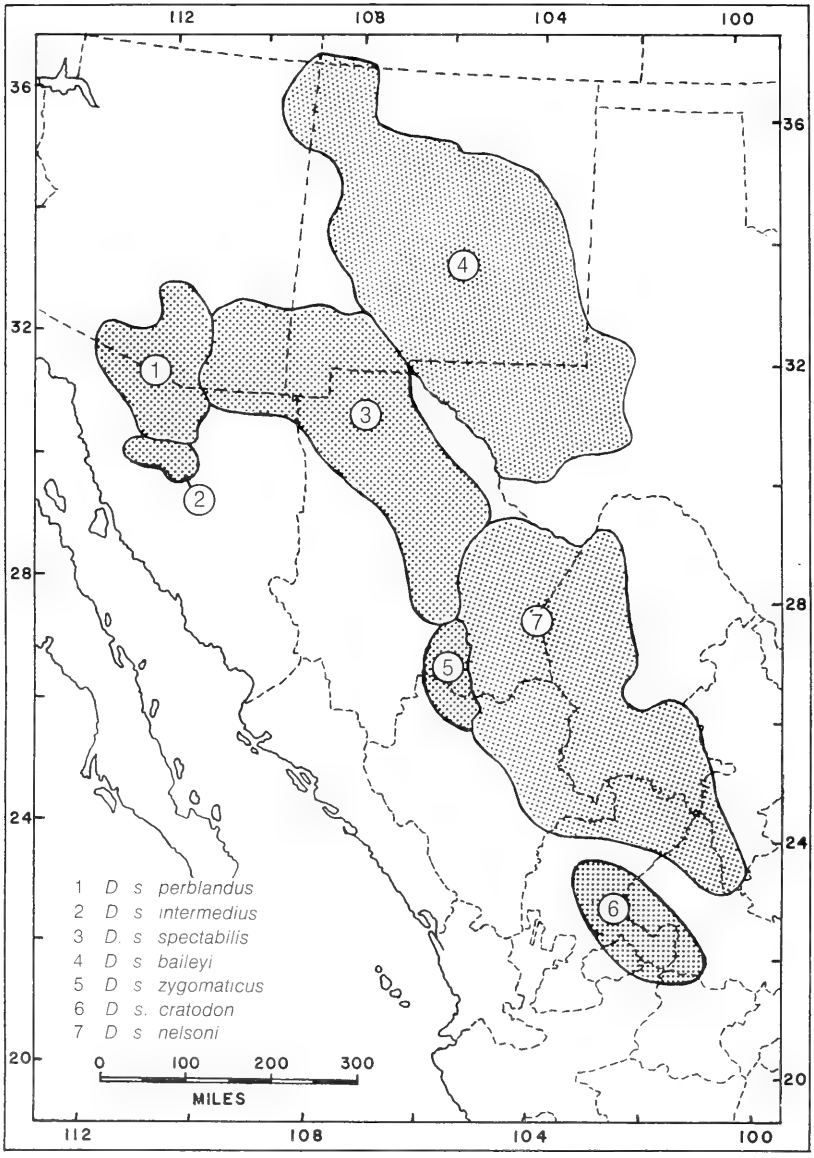


Fig. 2. Distributional range of the subspecies of *Dipodomys spectabilis.*

The external opening of the auditory meatus varies from round to oval in shape.

The hyoid apparatus is composed of only two parts, basihyal and a reduced thyrohyal, and is characterized as follows: the basihyal is medium-sized with a prominent ventral ridge. The anteromedial border of the "shoulders" is somewhat round. The basihyal arch is not so deep as in *D. deserti*. The thyrohyal is medium in size.

D. spectabilis primarily inhabits the upper edges of the Lower Sonoran Life-zone, but occasionally is found also in the Upper Sonoran Life-zone (Fig. 2). It prefers open sites with vegetation consisting of mixed grasses and desert shrubs such as mesquite, *Prosopis* sp., and creosote bush, *Larrea* sp.

Other kangaroo rats that range sympatrically with and share almost the entire range of *D. spectabilis* are *D. merriami* and *D. ordii*. Because it is larger in size, darker in coloration, and has the white tip on the tail, *D. spectabilis* can be differentiated easily from the other species.

Little is known about the longevity of *D. spectabilis*. Bailey (1931: 254) reported that a captive pair lived several years. A male (USNM No. 246652) kept in captivity for almost three years died presumably of old age.

Several species of carnivores, owls, and snakes prey on *D. spectabilis*. The badger, *Taxidea taxus*, and the kit fox, *Vulpes macrotis*, are the most important predators. Others cited by Vorhies and Taylor (1922:35) are the bobcat, *Lynx rufus baileyi*, the coyote, *Canis latrans*, skunks, *Mephitis* sp., the western horned owl, *Bubo virginianus*, and the barn owl, *Tyto alba*. Rattlesnakes, *Crotalus* sp., gopher snakes, *Pituophis* sp., and racers, *Masticophis flagellum*, may also be among *D. spectabilis* predators. Despite all these natural enemies, the number of kangaroo rats taken must be relatively small; the abundance of the species seems little affected, since the reproductive rate is comparatively low (*see* Reproduction, p. 12).

D. spectabilis is known to be the host for at least one species of flea, *Ctenophthalmus* sp., and one species of chigger, *Trombicula* sp. (Vorhies and Taylor, 1922). No record of endoparasites was found.

Of the 1,187 specimens of *D. spectabilis* examined in this study, only 114 showed any evidence of molting. Patterns of molting in these specimens were recorded. No juvenile molt was observed and only two immatures were molting, one in August and the other in September (Table 1). Subadult molt commences late in the spring and ends early in the winter with a peak in August. Adult molt was observed at least once in every month; however, adults seem to molt once a year—mostly

TABLE 1
Number of molting individuals of *Dipodomys spectabilis*
(by age-groups and month of capture)

	Month of capture											
Age-Group	J	F	M	A	M	J	J	A	S	O	N	D
Immature	—	—	—	—	—	—	—	1	1	—	—	—
Subadult	—	—	—	—	3	2	6	13	7	—	3	—
Adult	1	1	2	4	7	8	9	25	12	1	7	1

in August—as only a single peak in molting was observed. New hair first appears on the snout and cheeks, then proceeds posteriorly to the level of the ears; usually an area of unmolted hair is left between the eyes and this disappears later. Then, a saddle-shaped area of new hair appears in the middorsal region. From this area, molt progresses anteriorly to meet with the molted area in the head region behind the eyes. Later, molt proceeds laterally to the shoulders and sides, and then posteriorly to the rump and hind limbs.

REPRODUCTION

In 151 female kangaroo rats examined for pregnancy, placental scars, or lactation, only 45 showed these signs of reproduction (29.8%). Sexual maturity is attained late in the subadult age range (Table 2). Only five of 34 subadult females examined showed signs of reproductive activity (14.7%).

TABLE 2
Distribution of recorded reproductive activity in females of *Dipodomys spectabilis* by age-groups

	Immature	Sub-adult	Young Adult	Adult	Total
Females examined	5	34	41	71	151
Females showing reproductive activity	0	5	12	28	45

Reproductive activity takes place almost the year around, except perhaps in October and November. This activity evidently starts and terminates about a month earlier in the northern populations, which include *D. s. perblandus*, *D. s. intermedius*, and *D. s. spectabilis* (none

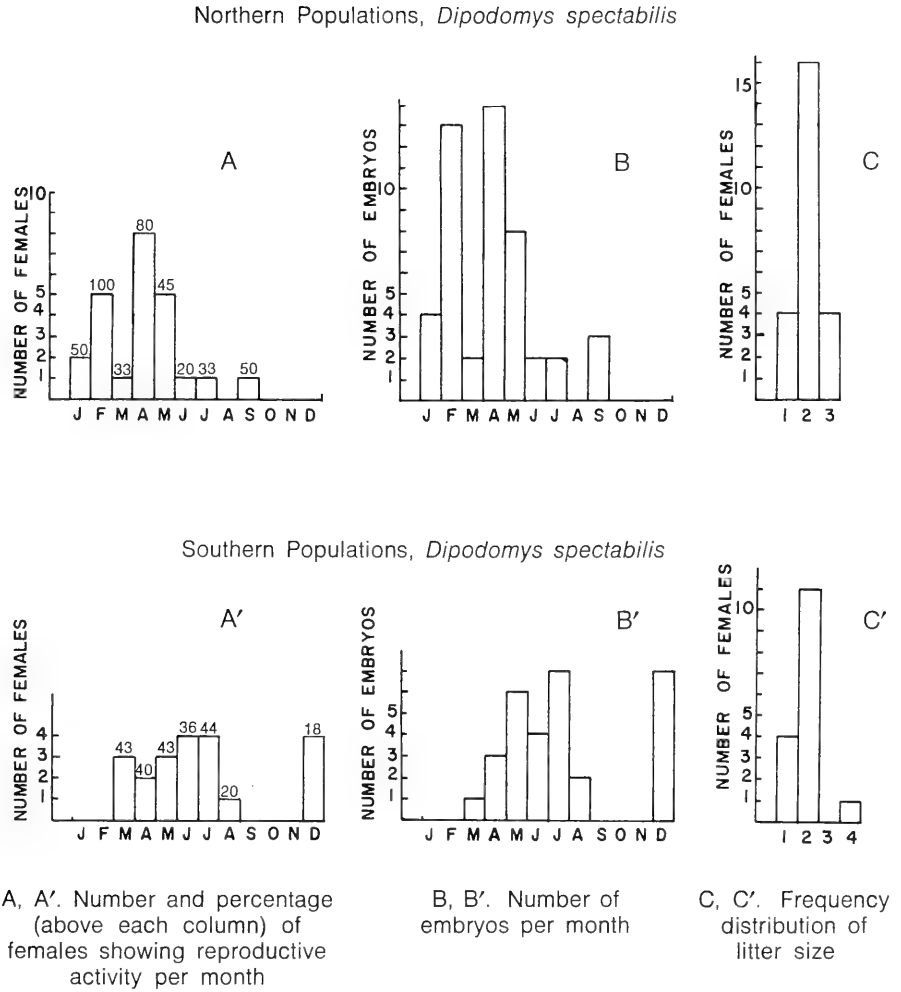


Fig. 3. Reproductive activity in the northern and southern populations of *Dipodomys spectabilis*.

examined for *D. s. baileyi*), than in the southern populations, which include *D. s. zygomaticus, D. s. cratodon,* and *D. s. nelsoni.* In the northern populations, breeding activity starts in December and ends late in September (Fig. 3A). No pregnant female was recorded in December. The earliest recorded pregnancy was on 10 January and the latest on 8 September (3 embryos × 10 mm). No record of pregnancy in August is available, although females were examined during this month.

In the southern populations, breeding starts late in November and ends in early September (Fig. 3A′). No pregnancy was recorded in November, but a young adult female collected on 1 December was carrying an embryo 10 mm in length. The latest recorded pregnancy in this group was on 26 August (2 embryos × 21 mm). The fact that, in this southern group, no pregnant females were found in January and February, may possibly indicate that too small a sampling of female rats was taken during these months. One female examined on 11 March was lactating. Although no pregnant female of *D. s. baileyi* was examined in this study, the data presented by Holdenried (1957) for this subspecies fit well within the present findings.

The largest number of pregnant females in the northern populations was in April, when 80% were pregnant (Fig. 3A). All females examined in February were pregnant. In the southern group, the months of December, June, and July showed the largest number of pregnant females (Fig. 3A′). The number of embryos counted was largest in April in the northern group, but in December and July in the southern group (Fig. 3; B, B′).

Reproductive activity in *D. spectabilis* is long, extending over a 10-month period and results in two, and possibly three, litters per year, at least in some subspecies (Holdenried, 1957). For my sample, the number of embryos in a litter ranges from 1 to 3 (mean 2.0) in the northern group and from 1 to 4 (mean 1.87) in the southern group (Fig. 3; C. C′) with a mode of 2 for both. Holdenried (1957:342) reported that in 12 females of *D. s. baileyi* with 33 embryos, the litter size ranged from 2 to 4 with an average of 2.75 per litter. Vorhies and Taylor (1922:18) reported that 67 females of *D. s. perblandus* had 122 embryos or placental scars, having a mean of 1.82 per female and a mode of 2. The differences in the mean of embryos per litter for northern populations as given by Holdenried (2.75) and my study (2.0) are probably accidental because of sample size.

There is little information concerning growth and development. The largest embryo recorded had a crown-rump length of 60 mm.

From Bailey's (1931) observations of a captive female *D. s. spectabilis,* the gestation period was found to vary between 22 and 27 days. Bailey also noted that the incisors erupted 11 days after birth and weaning took place between 20 and 25 days of age. Young males grow faster, in terms of weight, than young females (Holdenried, 1957:344).

COLOR

Variation in color of the pelage of *D. spectabilis* throughout its range is not great. The color of the upper parts, in general, is Light Ochraceous-Buff mixed with variable numbers of black-tipped hairs, depending on the subspecies. The coloring is purest on the sides and lightest on the cheeks. The black-tipped hairs are longer and coarser than the rest of the hairs of the dorsum. Samples from a given locality are quite uniform in color. Also, color of the upper parts within a given subspecies is stable.

The upper parts are thinly mixed with long black-tipped hairs in *D. s. perblandus, D. s. intermedius, D. s. nelsoni,* and *D. s. cratodon,* whereas the upper parts are heavily mixed with black-tipped hairs in *D. s. spectabilis* and *D. s. zygomaticus,* and moderately in *D. s. baileyi.* The pure color of the upper parts in *D. s. intermedius* is lightly mixed with Pinkish Buff which is more evident on the sides, while in *D. s. baileyi* it is occasionally mixed with Pinkish Buff, especially among the populations in western Texas; in *D. s. nelsoni* it is occasionally mixed with grayish hairs.

The different subspecies do not exhibit noticeable variation in the whitish area between the arietiform markings and the eye, the supraorbital and postauricular spots, hip stripe, color of the ventral surface, fore feet, dorsal surfaces and sides of hind feet, the incomplete ring at the base of the tail, and the lateral tail stripes. Color variation is, however, noticeable in the following: the arietiform markings and the anterior ear fold are dusky in *D. s. perblandus, D. s. intermedius,* and *D. s. nelsoni*; blackish in *D. s. baileyi*; black in *D. s. spectabilis* and *D. s. zygomaticus. D. s. cratodon* has dusky arietiform markings and a black anterior ear fold. The large dark spot behind the ankle varies from dusky to black and occasionally is mixed with gray. The plantar stripe varies from light brown to dark brown to black; the lightest is in *D. s. intermedius,* the darkest in *D. s. spectabilis.* The ventral surface of the toes is usually washed with yellowish or brownish color. The subterminal band of the tail is blackish in *perblandus, intermedius, nelsoni,* and *cratodon*; black in *spectabilis, baileyi,* and *zygomaticus.* Although the length of the white tip of the tail is variable

within the subspecies as well as among the different subspecies, it is long in *spectabilis* and *baileyi*; short in *intermedius* and *perblandus*; shortest in *D. s. nelsoni*.

Age Variation

Five age-groups of *D. spectabilis* are recognized. Although these divisions are arbitrary (as no individual of exactly known age was available), they nevertheless serve to categorize the available material and facilitate comparisons of individuals of similar ages.

Juvenile. Deciduous teeth PM4, pm4 are present and show some or considerable wear. M1-2, m1-2 show some wear. M3, m3 are either just erupted or not yet erupted (Fig. 4; a, a′, b, b′). M3 may show slight wear in the older juveniles, but m3 shows no wear in any of the specimens examined. The two lophs on the crown of M3 are still evident in old juveniles (Fig. 4; c, c′). The skull, in general, is fragile and the dorsal surface is convex. The auditory bullae are opaque and rough. The color of the pelage is more grayish than ochraceous and the fur is short, especially on the tail. The dorsal and ventral tail stripes are black in their entire length. The tail is not penicillate.

Immature. Deciduous PM4, pm4 have just been shed. M3, m3 show some wear in the youngest animals (Fig. 4; d, d′). In old immatures, the permanent PM4 shows some wear, and pm4 shows slight wear. The two lophs of the permanent PM4 are still evident. The molars are acquiring an oval shape on the occlusal surface (Fig. 4; e, e′). The dorsal surface of the skull is convex and the auditory bullae are still opaque and rough. The color is slightly more ochraceous, and the fur is slightly longer than in the juveniles. The distal part of the dorsal tail stripe is darker than its proximal part. The tail is becoming penicillate.

Subadult. Permanent dentition is present and all teeth show some wear. All cheek teeth are acquiring a more oval shape, except M3 which usually appears somewhat "triangular" in shape with its apex pointing posteriorly, and pm4 which is almost rectangular in shape (Fig. 4; f, f′, g, g′). Enamel breaks—absence of the enamel from either the lingual side or the labial side or both—appear in this age group and are present in all cheek teeth of older subadults. The auditory bullae are still rough, opaque, and porous. The hair is still grayish, but otherwise assuming adult coloration.

The youngest subadult (Fig. 4; f, f′) shows a shallow groove in the

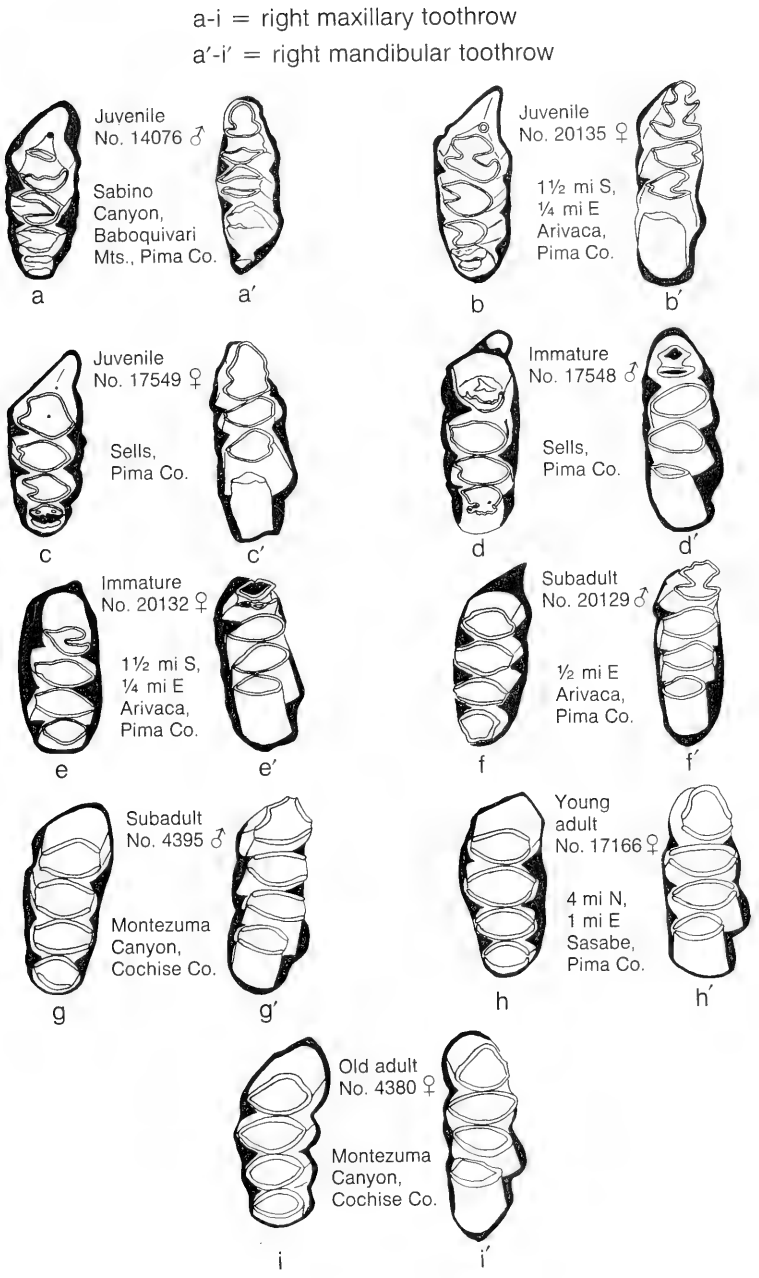


Fig. 4. Occlusal views of molariform teeth of different age groups of *Dipodomys spectabilis* in Arizona. All specimens are from UI Collection.

anteromedial surface of PM4. This indicates the remains of the enamel infolding that separates the protoloph from the metaloph (see Dentition). In pm4 of the same specimen, a labial and a lingual infolding are still present, and in many cases in other specimens a frontal groove also is present. Enamel breaks first develop in M1 and M2, later in PM4, and lastly in M3. The development of enamel breaks in the mandibular teeth follows the same pattern. In the youngest subadults, enamel breaks are absent in PM4, pm4. In older subadults, two enamel breaks, a lingual and a labial, are present in each tooth. Some pm4s however, may have three or sometimes four enamel breaks (Fig. 4; g, g').

Young Adult. Cheek teeth have an oval shape, except pm4, which has a rectangular or occasionally a "triangular" shape (Fig. 4; h, h'). Enamel breaks are present in all or any one of the cheek teeth. The auditory bullae are shiny and smoother than those of the subadults. The color of the pelage attains its adult condition in this age-group (see Species Characteristics, p. 9).

In younger young adults, all cheek teeth have enamel breaks which tend to get narrower in older specimens and disappear in some teeth in the oldest young adults. Enamel breaks disappear first in M2 and M3, then in M1 and PM4. Lower teeth follow the same general pattern.

Old Adult. All teeth show much wear and pm4 is more "triangular" than rectangular in shape (Fig. 4; i, i'). The enamel breaks in all cheek teeth have disappeared. The auditory bullae are shinier and are usually translucent.

To determine whether differences between means of the young adult and the old adult age-groups were significant, localities from 23 to 35 mi S Tucson and 27 to 30 mi SE Tucson, Pima County, Arizona, were grouped, resulting in a series of 42 specimens; 26 males (9 young adults and 17 old adults), and 16 females (8 young adults and 8 old adults). The means of 19 measurements of two age-groups within each sex were compared. In both sexes, old adults were slightly larger than the young adults in about half of the measurements (Table 3). The differences between the means were not statistically significant and accordingly these two age-groups were combined for further analysis and were called the adult age-group.

DENTITION

The sequence of tooth eruption in the upper jaw in *D. spectabilis* is as

TABLE 3

Comparisons between "young adult" and "old adult" age-groups of *Dipodomys spectabilis*[a]

(The order is mean, number of specimens as a superscript, one standard deviation, and one standard error of mean. Measurements are in mm)

Character	Males		Females	
	"Young adults"	"Old adults"	"Young adults"	"Old adults"
Total length	332.8^{8}	325.5^{11}	323.0^{7}	325.5^{8}
	15.13 ± 5.36	13.77 ± 4.15	6.35 ± 2.40	11.72 ± 4.14
Tail length	195.3^{9}	187.9^{11}	189.4^{7}	193.5^{8}
	11.28 ± 3.76	11.29 ± 3.40	6.66 ± 2.52	7.39 ± 2.61
Hind foot length	50.1^{9}	49.9^{16}	49.5^{8}	49.1^{8}
	1.06 ± .353	2.15 ± .537	1.51 ± .534	1.81 ± .638
Ear length	15.0^{1}	15.5^{10}	17.0^{1}	16.4^{5}
	—	.71 ± .223	—	1.14 ± .509
Body length	135.2^{8}	135.9^{15}	136.0^{8}	132.0^{8}
	8.41 ± 2.97	7.02 ± 1.81	4.44 ± 1.57	5.93 ± 2.10
Greatest skull length	44.3^{8}	44.7^{16}	44.1^{8}	44.0^{6}
	.78 ± .275	1.03 ± .257	1.11 ± .391	.74 ± .30
Basal skull length	32.3^{9}	32.5^{16}	32.3^{7}	31.8^{6}
	.70 ± .235	.62 ± .155	.83 ± .313	.54 ± .218
Length of nasals	15.9^{8}	16.3^{17}	16.1^{8}	16.3^{8}
	.46 ± .162	.55 ± .134	.48 ± .169	.58 ± .204
Breadth across max. arches	25.8^{9}	26.2^{15}	25.8^{8}	26.1^{8}
	1.29 ± .429	.60 ± .153	.63 ± .222	1.10 ± .70
Least interorbital breadth	15.0^{7}	15.3^{16}	14.9^{6}	15.5^{8}
	.76 ± .288	.50 ± .126	.28 ± .113	.83 ± .292
Greatest breadth across bullae	28.8^{8}	28.6^{15}	28.3^{8}	28.2^{6}
	.78 ± .276	.63 ± .161	.73 ± .258	.62 ± .254
Rostral breadth	4.5^{7}	4.6^{17}	4.6^{8}	4.5^{8}
	.18 ± .066	.24 ± .057	.23 ± .079	.21 ± .073
Rostral depth	8.5^{9}	8.5^{17}	8.5^{8}	8.4^{8}
	.35 ± .117	.27 ± .065	.18 ± .065	.22 ± .078
Bullar depth	14.9^{8}	15.1^{16}	14.9^{8}	14.9^{7}
	.16 ± .055	.43 ± .107	.42 ± .149	.34 ± .128
Alveolar length of max. toothrow	6.0^{9}	6.0^{17}	5.9^{8}	5.8^{8}
	.24 ± .079	.30 ± .071	.37 ± .13	.26 ± .092
Least breadth of supraoccipital	2.2^{9}	2.1^{16}	2.1^{8}	2.2^{6}
	.48 ± .158	.30 ± .073	.45 ± .159	.38 ± .156
Breadth across exoccipitals	14.0^{9}	13.9^{15}	13.8^{6}	13.5^{6}
	.61 ± .204	.43 ± .112	.51 ± .211	.44 ± .18
Alveolar length of mand. toothrow	5.8^{9}	5.8^{17}	5.7^{8}	5.8^{8}
	.22 ± .071	.20 ± .048	.34 ± .121	.22 ± .077
Mandibular length	18.9^{9}	19.1^{17}	18.7^{8}	19.0^{8}
	.27 ± .091	.60 ± .145	.26 ± .09	.45 ± .16
Length of white tip of tail	24.7^{6}	24.3^{8}	22.6^{5}	25.7^{7}
	4.84 ± 1.976	2.31 ± .819	4.97 ± 2.22	4.63 ± 1.75

[a]From 23 to 35 mi S Tucson and 27 to 30 mi SE Tucson, Pima Co., Arizona.

follows: The deciduous incisors, although not seen in any of the specimens examined, are regarded as the first teeth to erupt from the alveolar ridge, and are lost very shortly thereafter. Bailey (1931:256) noted in captive animals that at 11 days of age, the permanent incisors first appeared through the gums as hard points or edges. The deciduous PM4 which shows slight wear in the youngest juvenile is assumed to have erupted shortly after the incisors erupted, probably at 13 or 14 days of age. Deciduous PM4s persist for a short period before being lost. M1 evidently erupts at the same time as the deciduous PM4 or shortly thereafter, as it exhibits slight but comparable wear. Both deciduous PM4 and M1 show some wear before the eruption of M2. The latter shows some wear before the eruption of M3 which exhibits some wear before the deciduous PM4 is lost. The last tooth to erupt is the permanent PM4 which can be seen between the roots of the deciduous PM4 in older juveniles.

The sequence of eruption in the lower jaws follows the same general pattern as that of the upper jaws, except that the permanent incisors and m3 are slower in eruption and development. No wear was observed in m3 before the loss of the deciduous pm4. The permanent pm4 is slower in development and wears more slowly than the permanent PM4.

In the youngest juvenile examined, both deciduous PM4 and pm4 are slightly worn and their cusps are not clearly evident. Deciduous PM4 has an anterior cusp, which has already lost its enamel covering, followed by a transverse protoloph near the middle and a metaloph at the posterior end of the tooth (Fig. 4a). Then the protoloph unites with the metaloph at the middle, forming an H pattern, with a deep lingual and a shallow labial enamel infolding (Fig. 4b). Later, the anterior cusp unites with the protoloph. The deciduous PM4 shows less wear than that of pm4. In pm4 there is also an anterior cusp and two transverse lophids: a protolophid near the middle and a metalophid near the posterior end. At this early stage, the anterior cusp has already united with the protolophid at the middle, leaving a deep lingual and a shallow labial enamel enfolding (Fig. 4a′). Later, the metalophid unites with the protolophid at the middle, resulting in an additional labial and lingual enamel infolding (Fig. 4b′).

All permanent teeth have two lophs or lophids. The lophs of PM4 unite at the labial side, leaving a deep lingual enamel infolding (Fig. 4a), while the lophids of pm4 unite at the middle of the tooth, leaving two deep enamel infoldings, a labial and a lingual (Fig. 4f′). The two lophs and lophids of both upper and lower molars unite lingually

leaving deep labial enamel infoldings. Moreover, only M3 has a shallow indentation on the lingual side, and all lower molars have a shallow lingual infolding.

Of the specimens examined, several from discrete parts of the range of the species have lower incisors with a shallow-grooved, anterior face, although there was no uniform pattern or subspecific correlation in their presence. They probably represent independent mutations.

Individual Variation

In a sexually reproducing population, individual variation is expected, but the twenty measurements studied in *D. spectabilis* show no great variability for either males or females, except for the least supraoccipital breadth and the length of the white tip of the tail. Table 4 shows

TABLE 4

Coefficients of variation in two grouped localities of *Dipodomys spectabilis* from Arizona

Character	*D. s. perblandus*[a] 26 ♂ ♂	16 ♀ ♀	*D. s. spectabilis*[b] 19 ♂ ♂	16 ♀ ♀
Total length	4.38[19]	2.87[15]	3.02	3.58[15]
Tail length	6.08[20]	3.72[15]	4.18	6.07[15]
Hind foot length	3.62[25]	3.31	3.27	3.24
Ear length	7.86[11]	6.62[6]	5.32	7.21[15]
Body length	5.32[23]	4.64	3.62	5.81[14]
Greatest skull length	2.14[24]	2.12[14]	2.31	2.55
Basal skull length	1.35[25]	2.28[13]	2.52	2.65
Length of nasals	3.32[25]	3.25	3.40	2.62
Breadth across maxillary arches	3.45[24]	3.39	2.93[18]	3.20
Least interorbital breadth	3.88[23]	4.55[14]	4.64[18]	4.95
Greatest breadth across bullae	2.35[23]	2.33[14]	2.60	2.93[15]
Rostral breadth	4.88[24]	4.59	5.62	6.99
Rostral depth	3.46	2.35	3.14	2.66
Bullar depth	3.70[24]	2.52[15]	2.15	2.02
Alveolar length of maxillary toothrow	4.51	5.18	4.65	4.06
Least breadth supraoccipital	14.02[25]	18.98	16.38	15.43
Breadth across exoccipital	3.58[24]	3.65[12]	3.27	3.03
Alveolar length of mandibular toothrow	3.45	4.97	3.55	4.05
Mandibular length	2.62	1.97	2.63	3.05
Length of white tip of tail	14.16[14]	19.80[14]	21.42	12.11[15]

[a]23 to 35 mi S Tucson and 27 to 30 mi SE Tucson, Pima County.

[b]5 to 20 mi SE Fort Huachuca, Cochise County.

the coefficients of variation for two grouped localities representing two different subspecies.

The high degree of variation in the supraoccipital breadth was also noted by Lidicker (1960:140) in his study of Merriam's kangaroo rat. I agree with Lidicker in attributing this high variability to the dependence of the width of the supraoccipital on bullar inflation. This inflation tends to reduce the size of both the supraoccipital and the interparietal from two directions. The interparietal is also highly variable and probably tends to be eliminated inasmuch as the presence of more than one interparietal, its fusion with the supraoccipital, or sometimes its absence, are indications of its instability. More than one interparietal may indicate the presence of more than one center of ossification, and the failure of these centers to coalesce produces the multiplicity of bones. Absence of the bone results from one of two factors: either it is not developed originally, which allows the arms of the supraoccipital to fuse together, or the interparietal is fused indistinguishably with the supraoccipital, although its place is still evident. The absence of the interparietal is neither a function of aging since it remains distinct in skulls of aged animals, nor it is a function of hypertrophy of the bullae, for they rarely are inflated enough to overcrowd the interparietal as in *Dipodomys deserti*. Ordinarily the interparietal is elongated in shape, except in *D. s. perblandus* in which it is generally diamond-shaped.

The great variation in the measured lengths of the white tip of the tail is partly a result of inaccurate measuring.

In general, external measurements vary more than cranial measurements, especially tail length and ear length, because different collectors use different techniques in making these measurements. Rostral width and alveolar length of the maxillary toothrow are highly variable cranial dimensions.

The mean of the alveolar length of the maxillary toothrow was compared with that of the mandibular toothrow in both of the above-mentioned grouped localities. For both males and females in the two groups, the maxillary is longer than the mandibular toothrow. In the first group, the difference is significant in males, but not in females. In the second group, the differences are not significant in either sex.

Secondary Sexual Dimorphism

Males usually are slightly but not significantly larger than females. To analyze secondary sexual dimorphism, two grouped localities were used. Group A was the same one used in the age-group analysis. Group

B was from 5 to 20 mi SE Fort Huachuca, Cochise County, Arizona. In Group A the means of 13 of the 20 measurements compared were slightly larger in the males than those of the females (Table 5). In Group B, the means of nine measurements were slightly larger in the males (Table 5). However, none of the means of the 20 measurements of the males was significantly different from those of the females in either group. Accordingly, the two sexes were combined for the analysis of differences between the means of the different populations.

Geographical Variation

Morphological variation among the different populations of *D. spectabilis* throughout the range of the species is evident. This variation is caused partly by some habitat differences in the different parts of the range and partly by geographic isolation and the presence of some partially effective barriers.

Geographically, the most variable measurements are total length, tail length, greatest skull length, and, to a lesser degree, basal length, nasal length, greatest breadth across the bullae, bullar depth, and mandibular length. Similarly, the least variable measurements are alveolar length of the maxillary toothrow, least supraoccipital breadth, greatest breadth of the exoccipitals, and alveolar length of the mandibular toothrow.

There is some pattern in the variation throughout the range of the species. *D. s. spectabilis*, which is almost in the center of the range, is medium in size in almost all the measurements. The western populations, *D. s. perblandus* and *D. s. intermedius*, are smaller in most of the characters than *D. s. spectabilis*. However, *D. s. intermedius* is generally smaller than *D. s. perblandus*. The populations of *D. s. baileyi* in the northeastern part of the range have the largest measurements of most of the characters. Specimens from some localities in western Texas are in some characters similar to those of *D. s. spectabilis*. Although the populations of *D. s. zygomaticus* in south central Chihuahua and north central Durango are sufficiently differentiated from *D. s. spectabilis* to the north, the differences are not great. The smallest and most distinct populations are those in the east-southeastern part of the range, *D. s. nelsoni* (see also the account of this subspecies p. 56). The disjunct populations of *D. s. cratodon* in the southeasternmost part of the range are distinct and usually larger than *D. s. nelsoni*. However, in some characters they are similar to those of *D. s. spectabilis*.

No clinal change throughout the range of the species is clear in any

TABLE 5

Comparison between adult males and adult females from two grouped localities of *Dipodomys spectabilis* from Arizona

(Number of individuals, mean, range, one standard deviation, and one standard error of the mean. Measurements in mm)

Character	Group A[a]		Group B[b]	
	26 ♂ ♂	16 ♀ ♀	19 ♂ ♂	16 ♀ ♀
Total length	328.53[19]	324.33[15]	339.58	338.27[15]
	(312.0-350.0)	(312.0-346.0)	(325.0-358.0)	(317.0-361.0)
	14.43	9.369	10.319	12.151
	±3.311	±2.419	±2.367	±3.138
Tail length	191.25[20]	191.6[15]	195.74	196.2[15]
	(170.0-212.0)	(178.0-203.0)	(178.0-207.0)	(175.0-212.0)
	11.62	7.119	8.217	11.893
	±.447	±1.779	±1.886	±3.071
Hind foot length	49.98[25]	49.31	53.69	53.0
	(45.0-55.0)	(47.0-52.0)	(51.0-56.0)	(50.0-56.0)
	1.805	1.629	1.766	1.713
	±.361	±.407	±.405	±.428
Ear length	15.45[11]	16.5[6]	16.84	16.77[15]
	(15.0-19.0)	(15.0-18.0)	(15.0-19.0)	(15.0-19.0)
	1.217	1.095	.899	1.207
	±.367	±.447	±.206	±.312
Body length	135.74[23]	134.0	143.84	140.93[14]
	(120.0-146.0)	(124.0-143.0)	(131.0-151.0)	(125.0-155.0)
	7.22	6.218	5.23	8.177
	±1.507	±1.554	±1.201	±2.186
Greatest skull length	44.54[24]	44.02[14]	45.51	45.38
	(42.7-47.3)	(42.5-45.9)	(43.4-47.1)	(42.4-46.7)
	.959	.94	1.048	1.152
	±.195	±.251	±.241	±.289
Basal skull length	32.41[25]	32.03[13]	33.35	33.36
	(31.4-33.2)	(31.3-33.7)	(32.0-35.0)	(31.4-34.5)
	.436	.737	.84	.887
	±.087	±.204	±.193	±.222
Length of nasals	16.18[25]	16.19	16.51	16.59
	(15.5-17.7)	(15.2-17.1)	(15.6-17.4)	(15.7-17.6)
	.537	.525	.561	.437
	±.107	±.131	±.129	±.109
Breadth across maxillary arches	26.01[24]	25.93[16]	26.02[18]	26.02
	(23.3-27.4)	(24.2-27.3)	(24.8-27.3)	(24.4-27.0)
	.901	.878	.761	.833
	±.184	±.219	±.18	±.209
Least interorbital breadth	15.23[23]	15.25[14]	14.73[18]	15.27
	(14.0-16.2)	(14.0-16.5)	(13.4-15.9)	(14.1-16.4)
	.593	.694	.686	.754
	±.123	±.185	±.161	±.189

Character	Group A[a]		Group B[b]	
	26 ♂ ♂	16 ♀ ♀	19 ♂ ♂	16 ♀ ♀
Greatest breadth across bullae	28.64[23] (27.7-29.7) .671 ±.14	28.21[14] (27.3-29.4) .661 ±.177	29.09 (27.6-30.6) .755 ±.173	29.35[15] (27.2-30.5) .866 ±.224
Rostral breadth	4.54[24] (4.1-5.0) .22 ±.045	4.53 (4.2-4.9) .208 ±.052	4.51 (4.0-5.0) .254 ±.058	4.56 (3.9-5.0) .317 ±.08
Rostral depth	8.52 (8.0-9.1) .294 ±.057	8.43 (8.2-8.8) .198 ±.049	8.66 (8.0-8.9) .274 ±.062	8.61 (8.3-9.1) .231 ±.058
Bullar depth	15.05[24] (14.4-16.0) .558 ±.114	14.89[15] (14.2-15.6) .378 ±.097	15.37 (14.9-15.9) .33 ±.076	15.39 (14.6-15.8) .31 ±.078
Alveolar length of maxillary toothrow	6.02 (5.4-6.4) .272 ±.053	5.81 (5.5-6.5) .302 ±.075	6.25 (5.7-6.9) .292 ±.067	6.23 (5.8-6.6) .253 ±.063
Least breadth supraoccipital	2.13[25] (1.6-2.8) .297 ±.059	2.17[14] (1.2-2.6) .412 ±.11	1.7 (1.2-2.2) .277 ±.064	1.8 (1.3-2.3) .278 ±.069
Breadth across exoccipitals	13.91[24] (13.2-15.3) .498 ±.101	13.65[12] (12.8-14.2) .497 ±.143	13.96 (13.0-14.9) .454 ±.104	13.86 (12.9-14.6) .42 ±.106
Alveolar length of mandibular toothrow	5.81 (5.5-6.1) .20 ±.039	5.74 (5.3-6.4) .285 ±.071	6.05 (5.7-6.4) .213 ±.05	6.01 (5.6-6.4) .243 ±.061
Mandibular length	19.03 (18.3-20.6) .497 ±.097	18.83 (18.3-19.6) .371 ±.092	19.94 (18.7-20.9) .527 ±.121	19.84 (18.7-20.9) .606 ±.151
Length of white tip of tail	24.43[14] (18.0-33.0) 3.46 ±.893	24.51[12] (15.0-33.0) 4.85 ±1.4	40.21 (20.0-55.0) 8.613 ±1.977	40.93[15] (33.0-49.0) 4.963 ±1.281

[a]*D. s. perblandus* from 23 to 35 mi S Tucson and 27 to 30 mi SE Tucson, Pima County.

[b]*D. s. spectabilis* from 5 to 20 mi SE Fort Huachuca, Cochise County.

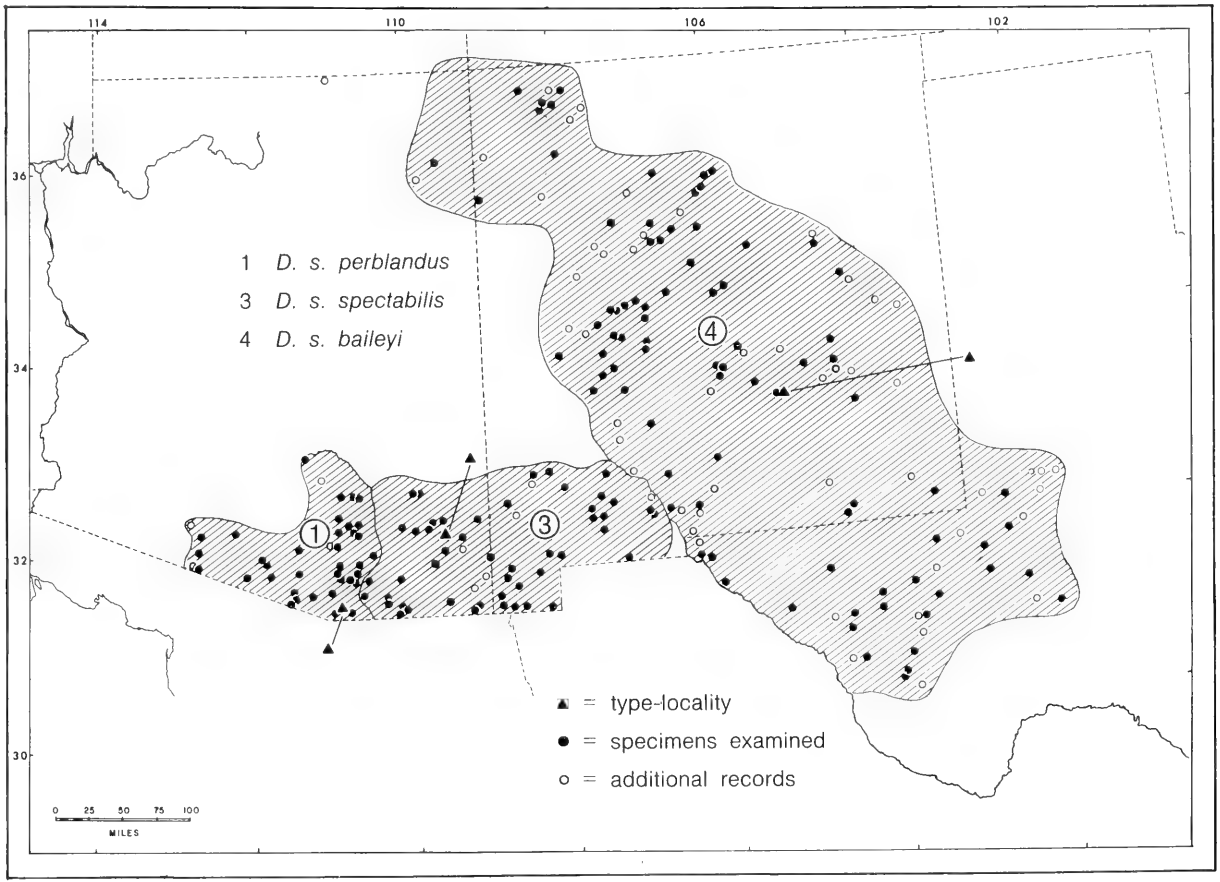


Fig. 5. Known occurrences and probable geographic range of the subspecies *Dipodomys*

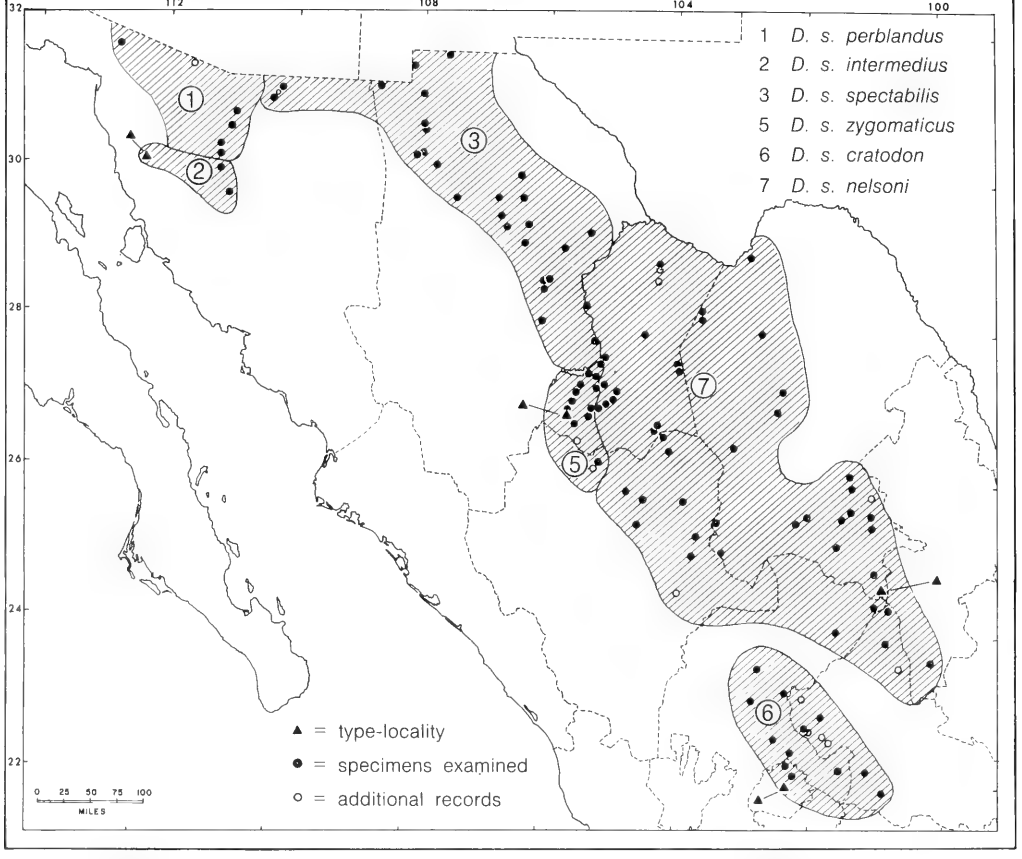


Fig. 6. Known occurrences and probable geographic range of the subspecies of *Dipodomys spectabilis* in Mexico.

of the measurements studied. However in a small part of the range in Arizona and Sonora, there is a southward clinal variation in some of the characters. The northern populations are usually larger.

The two smallest populations of the species are found on opposite sides of the Sierra Madre Occidental: *D. s. intermedius* on the western side and ***D. s. nelsoni*** on the eastern side. *D. merriami* also occurs on both sides, but Lidicker (1960) mentioned no similar situation in *D. merriami*. The southernmost populations on the western side of the Sierra, ***D. m. mayensis,*** are moderately small (Lidicker, 1960:185).

No correlation between nasal length and either rostral depth or rostral width or both was detected in *D. spectabilis*; in *D. deserti*, however, a north-south clinal change and a correlation between longer nasals and greater rostral depth were detected, presumably correlated with higher temperature and lower humidity (see Geographical Variation under ***D. deserti,*** p. 80).

SUBSPECIES OF *DIPODOMYS SPECTABILIS*

***Dipodomys spectabilis spectabilis* Merriam**

Dipodomys spectabilis Merriam, N. Am. Fauna, 4:46, 8 October 1890, original description.

[*Dipodomys spectabilis*] *spectabilis*: Merriam, Proc. Biol. Soc. Washington, 20:75, 22 July 1907.

Type. Male, young adult, skin and skull; No. 17886/24823, U. S. Biological Surveys Collection; from Dos Cabezos [=Dos Cabezas], Cochise County, Arizona; obtained by Vernon Bailey, 22 November 1889, original number 695.

Range. Southeastern Arizona, northeastern Sonora, southwestern New Mexico, northern and central Chihuahua.

More specifically, west from the eastern slopes of the Santa Rita Mountains, the vicinity of Fort Crittenden, Santa Cruz County, Arizona, and the vicinity of Cananea in northeastern Sonora, east to the western edge of the Rio Grande Valley in New Mexico and Chihuahua. Does not extend north beyond the valley south of the Gila River; northernmost known record is Fort Grant, Graham County, Arizona. In Chihuahua, not known from the immediate eastern slopes of the Sierra Madre Occidental but extends south and southeast to the western edge of the Rio Conchos. Limits of range are fairly well known except in the northeastern part in New Mexico, its eastern limit west of the Rio Grande in Chihuahua, the eastern side of the Sierra Madre Occidental, and along the western tributary of the Rio Conchos.

Diagnosis.

Size: Medium; adult total length 338.0 to 350.0 mm; tail length 197.0 to 206.2 mm; body length 141.0 to 146.3 mm; hind foot length 51.0 to 54.0 mm; ear length 16.8 to 18.0 mm; white tip of tail long, 30.0 to 44.0 mm.

Color: In general, Light Ochraceous-Buff, heavily mixed with

black tipped hairs on dorsum, purest on sides and lightest on cheeks; arietiform markings black; ear fold anteriorly black; large spot behind ankle blackish; plantar stripe dark brown to black, usually becoming light brown or yellowish on ventral side of toes; white band at base of tail interrupted by dusky or black tuft on ventral surface; dorsal and ventral tail stripes dusky; subterminal band of tail black.

Skull: Medium-sized; adult greatest length 45.3 to 46.2 mm; basal length 33.0 to 34.1 mm; length of nasals 16.4 to 17.3 mm; maxillary arch heavy, somewhat slanted posteriorly; posterolateral edge of maxillary arch slightly flared out; medial side of lacrimal usually narrower than lateral side; mastoidal bullae large; greatest breadth across bullae 29.0 to 29.7 mm; supraoccipital and interparietal narrow; least supraoccipital breadth 1.5 to 1.9 mm; pterygoid foramen usually oval and directed anterolaterally; incisors and molariform teeth medium in size; alveolar length of maxillary toothrow 6.1 to 6.5 mm; opening of external auditory meatus generally oval; mandibular length 19.1 to 20.0 mm. Also see Table 6.

Comparisons. Compared with *Dipodomys spectabilis perblandus, D. s. spectabilis* differs in the following: Larger and darker; all external measurements greater; arietiform markings more distinct; ear fold anteriorly more blackish; large spot behind ankle darker; plantar stripe and ventral surface of toes usually darker; tuft of hairs ventral to white band at base of tail more blackish; dorsal and ventral tail stripes darker; black subterminal band darker; white tip of tail longer; skull larger in size; auditory bullae larger; least supraoccipital breadth narrower; interparietal usually narrower; maxillary arch usually more slanted posteriorly and less angled to the long axis of skull; posterolateral edge of maxillary arch usually less flared out; lacrimal less uniform in width; incisors and molariform teeth somewhat larger; pterygoid foramen usually oval and directed anterolaterally; opening of external auditory meatus usually more oval than round.

Compared with *Dipodomys spectabilis baileyi, D. s. spectabilis* differs in the following: Smaller in total length, tail length, hind foot length, and body length; usually darker in color; arietiform markings darker; skull less massive; greatest length and basal length smaller; maxillary arches not so heavy and less flared out; teeth slightly smaller, especially incisors; rostrum relatively longer; rostral width slightly narrower; rostral depth slightly shallower; auditory bullae relatively as well as actually smaller; greatest breadth across bullae and bullar depth smaller; mandibular length shorter.

Compared with *Dipodomys spectabilis zygomaticus, D. s. spectabilis*

differs in the following: Longer body and longer white tip of tail; color of upper parts slightly paler, the buffy element less heavily mixed with black; skull usually with longer nasals; least interorbital breadth usually narrower; posterolateral edge of maxillary arch slightly less flared; auditory bullae usually less expanded in front of meatus; jugals usually parallel and less divergent posteriorly; pterygoid foramen usually rounder and more anterolaterally directed; rostral depth and least supraoccipital breadth usually narrower; breadth across exoccipital greater.

Compared with *Dipodomys spectabilis nelsoni, D. s. spectabilis* differs in the following: Larger in all external measurements; usually with longer white tip of tail; usually with more ochraceous buff color on dorsum; pelage more heavily mixed with black-tipped hairs; darker arietiform markings; darker subterminal band of tail; skull larger in almost all measurements; maxillary arches relatively as heavy but actually smaller; auditory bullae larger; upper incisors usually wider; mandible usually longer.

Remarks. Typical *Dipodomys spectabilis spectabilis* is characterized by a long distal white tip of the tail, the maxillary arch slanted posteriorly, and both the interparietal and supraoccipital narrow.

Some external and cranial characters of the type-specimen and some topotypes of *D. s. spectabilis* are not characteristic for the subspecies. Notably, in some topotypes, the anterior face of the maxillary arch is more angled relative to the long axis of skull and more flared out. Also the interparietal and least supraoccipital breadth in some is wide. Specimens from 19 mi W, 2 mi N Willcox, Cochise County, Arizona, are more typical.

Buffy spots are occasionally present on the ventral side in specimens from various localities throughout the range of this subspecies, and more so than in any other subspecies. Less frequently there is a streak of buff-colored hair on the ventral side.

A narrow, sharp zone of intergradation exists between *D. s. spectabilis* and *D. s. perblandus* along a line that extends down the east side of the Rincon, Empire, Santa Rita, and Patagonia mountains in Arizona and southward in northern Sonora. This zone seems to be one of secondary intergradation and shows a high degree of concordance in the characters examined. Specimens from the following localities in the zone of intergradation, when compared with typical *D. s. spectabilis*, have the following characteristics: Specimens from Empire Ranch, Pima County, Arizona, show some degree of intergradation in that most adults have smaller hind feet; some have a wider interparietal

and supraoccipital; and some have a shorter mandibular alveolus. Specimens from Fort Crittenden, Santa Cruz County; the vicinity of Bonita, Graham County; and the vicinity of Willcox, Cochise County, show little intergradation. Specimens from Fort Huachuca and vicinity, Cochise County, show some intergradation of characters as some have lighter arietiform markings and smaller external measurements. Some of these specimens have wider supraoccipitals, less breadth across the exoccipitals, more flared posterolateral edges of the maxilary arches, larger interparietal, and more uniform lacrimals. Some adults from Montezuma Canyon show intergradation in having more flared maxillary arches, more uniform lacrimals, rounder pterygoid foramina, narrower least interorbital breadth, and narrower breadth across the exoccipitals. Some specimens from La Sauceda, Sonora, show intergradation of characters, as evidenced by shorter tails, shorter mandibular alveolus, and wider supraoccipital.

D. s. spectabilis may intergrade with *D. s. baileyi* in west-central New Mexico between the Gila River and the Rio Grande, but little evidence of this process is observed in the available material. Some specimens from Mangas Valley, Grant County, have a slightly greater breadth across the maxillary arches and thus are closer to *D. s. baileyi.*

D. s. spectabilis intergrades with *D. s. baileyi* in a wide zone along the Rio Grande in south-central New Mexico. Only 11 of the 20 measurements studied show taxonomic differences between these two subspecies in this region. Specimens from both Lat. 31° 47′, Long. 107° 15′, Luna County, and from Camp near Lake Palomas, Chihuahua, have some characters close to *D. s. baileyi,* while other characters are close to *D. s. perblandus. D. s. spectabilis* is not known from the valley immediately west of the Rio Grande in northeastern Chihuahua. This gap may not be a true one and is probably due to the inaccessibility of the region. Although certain areas within this gap do not seem to be suitable habitat for this subspecies, future collecting in this region may yield some *D. s. spectabilis.*

Specimens from the southernmost part of the range of *D. s. spectabilis* in Chihuahua exhibit evidence of intergradation with *D. s. zygomaticus.* Adults from the vicinities of Parrita and Pozo Mangiay have some cranial characters close to those of *D. s. zygomaticus.*

D. s. spectabilis may intergrade with *D. s. nelsoni* in east-central Chihuahua. The available material from this region is scanty. Two adults, one from near Coyamé, and one from south of Hormigas, are smaller in some external and two cranial measurements than typical *D. s. spectabilis,* and are within the range of *D. s. nelsoni.*

Two adult females from 7 mi W, 2 mi S Casas Grandes, Chihuahua, KU Nos. 64083 and 64084, are clearly different from typical *D. s. spectabilis*, especially in skull characters. They are similar to *D. s. perblandus* in having pale dorsal color and short white tip of the tail. Averages of three external measurements and of eight cranial measurements are smaller than for *D. s. spectabilis*. They have smaller auditory bullae, have wider interparietals, and supraoccipitals, and are broader across the exoccipitals. The maxillary arches are more slanted posteriorly, and the external auditory meatus has a more oval-shaped opening. It is probable that this population will merit taxonomic recognition when more specimens are available.

Alvarez (1960:407) assigned specimens from La Sauceda, 15 mi NNE Cananea and from 9 mi N Cananea, Sonora, to *D. s. perblandus*. Examination of four specimens from the former locality and one specimen from 5 mi N Cananea, reveals that they are more typical of *D. s. spectabilis*. The subspecies *D. s. spectabilis* has not been reported previously from Sonora, although in distribution maps of the species, it was assumed to be present in the northeastern part of the state.

The last three localities listed under specimens examined from Luna County, New Mexico, are probably all the same.

Specimens examined. A total of 331 specimens from:

ARIZONA. PIMA COUNTY: Empire Ranch, E Santa Rita Mts., 4,632 ft, 4 (USNM); Empire Ranch, 50 mi E of S Tucson [=38 mi SSE], 1 (UCLA); 40 mi SE Tucson, at Rosemont, Santa Rita Mts., 4,700 ft, 1 (USNM). SANTA CRUZ COUNTY: Fort Crittenden, 4,800 ft, 3 (CAS). GRAHAM COUNTY: Fort Grant, 5 (USNM); 2 mi NW Bonita, Graham Mts., 3 (UI); 3 mi E Bonita, Graham Mts., 2 (UI). COCHISE COUNTY: 8 mi W Bowie, 1 (LACM); 5 mi NE Willcox, 1 (KU); 3 mi N, 2½ mi E San Simon, 1 (UI); 19 mi W, 2 mi N Willcox, 4 (UI); 10 mi W, 2 mi S Willcox, 2 (UI); Willcox, 4 (USNM); 4½ mi E, 2¾ mi S Willcox, 5 (UI); Dos Cabezos [= Dos Cabezas], 500 ft, 7 (MVZ), 17 (USNM); Fort Bowie, 7 (USNM); Chiricahua Mts., 1 (MVZ); 12 mi S Dos Cabezos [=Dos Cabezas], 1 (MVZ); 4½ mi E, 24 mi S Willcox, 6 (UI); 5 mi E Portal, 3 (UI); Fairbank, 7 (AMNH), 8 (FMNH); Fort Huachuca, 9 (USNM); 5 mi S Fort Huachuca [actually ESE], 7 (UI); 8 mi S Fort Huachuca [actually SE], 1 (UI); 5 mi W Herford, 2 (KU); 3 mi SW Herford, 2 (UI); Montezuma Canyon, Huachuca Mts., 15 (UI); Mouth Montezuma Canyon, Huachuca Mts., 3 (UI); Montezuma Canyon, 8 mi E, 14 mi S Fort Huachuca, 12 (UI); Montezuma Canyon, 20 mi S Fort Huachuca [actually 8 mi E, 14 mi S Fort Huachuca], 2 (UI); 9 mi

N Douglas, 1 (UI); 6 mi NE San Bernardino, 4,000 ft, 3 (USNM); S. B. Ranch [San Bernardino Ranch], 2 (FMNH); San Bernardino Ranch, 3 (AMNH), 9 (USNM); 18 mi E Douglas, 1 (UI).

SONORA. La Sauceda, 4,700 ft, 15 mi NNE Cananea, 4 (MVZ); 5 mi N Cananea, 4,750 ft, 1 (MVZ).

NEW MEXICO. GRANT COUNTY: Silver City, 14 (USNM); Mangos [=Mangas] Valley, Head of Mangos [=Mangas] Lake, 3 (USNM); White Water [=Whitewater], 1 (USNM); Hachita, 2 (USNM). HIDALGO COUNTY: 10 mi NW Lordsburg, 1 (LACM); 12 mi S (by road) Animas, 2 (UNM); Hatchet Ranch, 1 (USNM); 17 mi S, 2 mi W Animas, 4 (KU); Animas Creek, 17 mi (by road) S Animas, 3 (UNM); 18 mi S, 3.2 mi W Animas, 1 (UNM); Adobe Ranch, N base Animas Pk., 1 (USNM); 7.2 mi N Cloverdale, 1 (UNM); 4 mi N Cloverdale, 1 (UNM); T 33 S-R 19 W, Sec. 29 [about 1 mi NE Cloverdale], 1 (UNM); 36 mi S, 5 mi W Animas, 1 (UNM); T 33 S-R 20 W, Sec. 19 [1 mi NE Cloverdale], 1 (UNM); Upper Animas Valley, 36 mi S, 3 mi W Animas, 3 (UNM); 36.5 mi S, 8 mi W Animas, 1 (UNM); 3 mi W, 1 mi N San Luis Pass, 3 (UNM); Deer Creek, Culberson Ranch, 1 (USNM); 46 mi S (by road) Animas, 1 (UNM); Animas Valley, Lang Ranch, 1 (USNM); Dog Spring [skin tag: Grant Co.], 8 (USNM). SIERRA COUNTY: Lake Valley, 5,000 ft, 2 (USNM). LUNA COUNTY: Ft. Cummings, 1 (USNM); 12 mi S Nutt, 1 (USNM); 6 mi N Deming, 1 (USNM); Deming, 4 (USNM); 10 mi E Deming, 1 (USNM); Florida Mts., 10 mi S, 7 mi E Deming, 1 (UNM); Camp No. 4, near Carrizallilo Springs, 7 (USNM); Lat. 31° 47′ Long. 30° 1′ [Long. 107° 15′], Mex. Bound. Line, 4 (USNM); Lat. 31° 47′, Long. 30° 15′ [Long. 107° 15′], Mex. Bound. Line near Emory's 5th Mon., Mex. [=Monument No. 15], 1 (USNM); 50 mi W El Paso, Mon. No. 15, Mex. Bound. Line, 1 (USNM). DONA ANA COUNTY: 15 mi W Las Cruces, 5 (LACM); 12 mi WSW Las Cruces, 1 (MVZ).

CHIHUAHUA. Camp near Lake Palomus [=Palomas], 1 (USNM); Mesquite [=Mosquito] Springs, near Mex. Bound. Line, 2 (USNM); White Water [=Whitewater], Mex. Bound. Line, 5 (USNM); 3½ mi N, 1 mi W San Francisco, 5,100 ft, 1 (KU); 2½ mi N, ½ mi W San Francisco, 5,100 ft, 2 (KU); Rancho San Francisco, 5,100 ft, 2 (KU); Colonia Diaz, 4,750 ft, 1 (USNM); Vuelta de Alamos, 4,200 ft, 2 (KU); Corralitos, 2 (USNM); 17 mi N Nuevo Casas Grandes, 2 (UI); Casas Grandes, 2 (USNM); 1 mi W Casas Grandes, 5 (UI); 7 mi W, 2 mi S Casas Grandes, 2 (KU); 11 mi SE Nuevo Casas Grandes, 2 (UNM); 14.8 mi SE Nuevo Casas Grandes, 2 (UI); 10 mi NW Galeana, 1 (UI); 4 mi S, 1 mi E Moctezuma, 4,550 ft, 3 (KU); S edge Sierra Mojina, 5,200 ft, 24 mi W Gallego, 1 (MVZ); Gallego, 12 (USNM); 4.4 mi SE San Buenaventura

[=Buenaventura], 1 (UI); Arroyo del Nido, 27 mi SW Gallego, 6,500 ft, 2 (MVZ); 5 mi N Cerro Campana [at mouth of Cañon de Santa Clara, S end Sierra del Nido], 5,350 ft, 2 (MVZ); Ojo de Laguna, 5,200 ft, 25 mi S Galego [=Gallego], 4 (MVZ); 15 mi W, 6 mi S Coyamé, 5,500 ft, 1 (KU); Rancho La Campana, 1,470 m, 4 (AMNH); 38 mi N, 18 mi E Chihuahua [approx. 5 mi S Hormigas], 4,700 ft, 1 (KU); 4 mi N, 2 mi W Chihuahua, 4,750 ft, 1 (KU); 5 mi N, 6 mi E Chihuahua, 3 (UI); Chihuahua, 8 (USNM); 6 mi E, 1 mi S Chihuahua, 8 (UI); 5 mi SE Chihuahua, 5,250 ft, 1 (MVZ); 1 mi SW Pozo Mangiay, 5,200 ft, 30 mi S Chihuahua, 1 (MVZ); 2 mi W Parrita, 1 (KU).

Additional records. ARIZONA. GRAHAM COUNTY: SW slopes Graham Mts., near Fort Grant, 5,000 ft (Vorhies and Taylor, 1922:8); 1 mi E Bonita, about 4,600 ft (Hoffmeister, 1956:279). COCHISE COUNTY: 5 mi E Willcox, 1 (UM, Cockrum, 1960:144); Sulphur Springs Valley (Monson, 1943:98); San Simon Valley (Cahalane, 1939:430); 3/10 mi NW Portal, 1 (UA); Portal (Cahalane, 1939:431); 2 mi E Portal, 2 (UM, Cockrum, 1960:144); near Chiricahua, 1 (UA); 5 mi W Herford, 2 (UM, Cockrum, 1960:144); 3 mi W Herford, 6 (UM, Cockrum, 1960:144).

SONORA. 9 mi N Cananea (DGC, Alvarez, 1960:407).

NEW MEXICO. GRANT COUNTY: Burro Mts., 5,700 ft (Vorhies and Taylor, 1922:8). HIDALGO COUNTY: Lordsburg (Bailey, 1931:249); Playas Valley (Bailey, 1931:249); 6 mi E Cloverdale, 1 (NMSUWC); DONA ANA COUNTY: New Mexico State University Ranch, about 16 mi NW Las Cruces, on the Jornada Plains, 4,200 ft, 8 (NMSUWC).

Dipodomys spectabilis perblandus Goldman

Dipodomys spectabilis perblandus Goldman, J. Washington Acad. Sci., 23 (10):466, 15 October 1933, original description.

Type. Female, adult, skin and skull; No. 17748/24689, U. S. Biological Surveys Collection; from Calabasas [about 3,500 feet], Santa Cruz County, Arizona; obtained by Vernon Bailey, 27 October 1889, original number 611.

Range. South central Arizona and north central Sonora.

More specifically, in Arizona, from the vicinity of Oracle, Pinal County, and the western slopes of the Santa Catalina, the Santa Rita and the Huachuca mountains and the vicinity of Cerro Blanco, Sonora, west to Ajo and the Valley of the Ajo on the western slopes of the

Ajo Mountains, and the Sonoita Valley within the boundary of the Organ Pipe Cactus National Monument, Pima County, Arizona, and adjoining parts of Sonora. Not known from north of the Gila River in Arizona; the northernmost known record is Florence, Pinal County, and it extends south to about 20 miles south of Santa Ana, Sonora. Limits of range are fairly well known in Arizona, but may extend farther north beyond the Gila River. The eastern limits and especially the zone of intergradation with *D. s. spectabilis* in Sonora need to be clarified, also the western and southern limits in Sonora, especially the area of intergradation with *D. s. intermedius*.

Diagnosis.

Size: Small; adult total length 325.9 to 337.0 mm; tail length 190.0 to 196.4 mm; body length 133.7 to 140.0 mm; hind foot length 48.0 to 50.9 mm; ear length 15.0 to 16.4 mm; distal white of tail medium, 21.3 to 29.0 mm.

Color: In general, Light Ochraceous-Buff, thinly mixed with black-tipped hairs on dorsum, purest on sides and shoulders, lightest on cheeks; arietiform markings dusky; anterior ear fold dusky; large spot behind ankle grayish black; plantar stripe brown or light brown; toes ventrally light brown or yellowish; tuft of hairs at base of tail ventrally dusky or gray; dorsal and ventral tail stripes grayish black; subterminal band of tail nearly black.

Skull: Small-sized; greatest length 44.1 to 44.9 mm; basal length 31.6 to 32.5 mm; length of nasals 15.6 to 16.3 mm; maxillary arch forms an almost right angle with long axis of skull; posterolateral edge of maxillary arch flared out; lacrimal narrow and uniform; greatest breadth across bullae 28.0 to 28.9 mm; supraoccipital and interparietal wide; least supraoccipital breadth 2.0 to 2.5 mm; alveolar length of maxillary toothrow 5.6 to 6.0 mm; opening of external auditory meatus generally round; pterygoid foramen usually round; mandibular length 18.1 to 19.0 mm. Also see Table 6.

Comparisons. Compared with *Dipodomys spectabilis intermedius*, *D. s. perblandus* differs in the following: Color Light Ochraceous-Buff with no pinkish shade on the sides; total length and tail length greater; skull larger in almost all measurements, especially basal length, auditory bullae, breadth across bullae, least supraoccipital breadth, mandibular length; teeth slightly heavier; opening of external auditory meatus more round; jugals heavier.

For comparison with *Dipodomys spectabilis spectabilis*, see account of that subspecies (pp. 30 ff.).

Remarks. Typical *Dipodomys spectabilis perblandus* is characterized by Light Ochraceous-Buff color, thinly mixed with black-tipped hairs with a medium white tip of the tail, flared out maxillary arches, a wide interparietal and supraoccipital, and medium-sized teeth.

Although the zone of intergradation between *D. s. perblandus* and *D. s. intermedius* is not well defined, the available material shows some intergradation between these two subspecies in Sonora. One adult from 20 mi S Santa Ana has some cranial characters suggestive of *D. s. intermedius.*

D. s. perblandus intergrades, along a narrow zone, with *D. s. spectabilis* in eastern Arizona and eastern Sonora. Some of the specimens assigned here to *D. s. perblandus* from the following localities along the contact zone have some external and cranial characters close to those of *D. s. spectabilis*: The vicinity of Oracle, Pinal County; the vicinity of Fort Lowell, 8 mi E Fort Lowell; Tanque Verde; and Saguaro National Monument, 10 mi E Tucson, Pima County. One adult from Black Mountain, 10 mi S, 2 mi W Tucson, Pima County, has several external and cranial characters close to those of *D. s. spectabilis.* The lowland south of the Rincon Mountains and north of the Santa Rita Mountains provides a good opportunity for populations from the east and west sides of the mountains to interbreed. One adult from the north base of the Santa Rita Mountains, and some adults from east of Continental, Pima County, have deeper auditory bullae similar to those of *D. s. spectabilis.* One adult from Cerro Blanco, Sonora, has a wider rostrum, and two adults from Magdalena have slightly darker arietiform markings, and several cranial characters close to those of *D. s. spectabilis.*

A few specimens from various localities throughout the range of *D. s. perblandus* have either buffy spots or a buffy shade on the ventral surface. The frequency of occurrence of the buffy color in this subspecies is less than that in *D. s. spectabilis.*

Usually, the jugals of *D. s. perblandus* are parallel. However some adults from various localities throughout the range of this subspecies have bowed jugals which is a characteristic of *D. s. zygomaticus.* The presence of this character in some specimens of *D. s. perblandus* is most likely independent, because this subspecies is far removed geographically from *D. s. zygomaticus.*

Specimens from the westernmost localities of *D. s. perblandus* also exhibit some variation. Two adults from Gunsight, Pima County, compared with topotypes, have paler dorsal and ventral tail stripes, slightly paler upper parts, longer tails, and wider interparietals. They have

shorter bodies and are smaller in several cranial characters. Two adults from Pozo de San Emeterio, Sonora, average shorter in tail length, but have longer nasals, deeper rostrum, and deeper bullae than typical *D. s. perblandus*. These variations among specimens from the western limit of this subspecies are irregular and do not follow a uniform pattern.

The northernmost specimens of *D. s. perblandus* examined are from Florence, Pinal County, Arizona. Of four specimens in the AMNH collection that were collected by F. Terry on 27 March 1947, from Florence, two are *D. s. perblandus* and the other two are *D. deserti arizonae*. This record provides the only known evidence that these two species occur together. Unfortunately no field notes of Terry's were found to detect any habitat differences, although differences are expected. Recent collecting in the vicinity of Florence and directly north of it produced only *D. deserti arizonae*. This indicates that *D. spectabilis* does not occur farther north of Florence. It is possible that the specimens of *D. s. perblandus* in the AMNH collection were taken only in the vicinity of Florence, and in fact from south of the town.

A specimen in the USNM collection, No. 229351 ♂, from Indian Oasis, Pima County, Arizona, was collected by A. B. Howell on 9 July 1918, original number 173. The skin of this specimen is typical of *D. s. perblandus*, but the cranium is more typical of *D. deserti arizonae* whereas the lower jaw is typical of *D. spectabilis*. Another specimen in the same collection (No. 229343 ♂, from Gila Bend, Maricopa County, Arizona, collected by A. B. Howell on 22 June 1918, original number 126) is a skin typical of *D. d. arizonae*, but it has a skull typical of *D. s. perblandus* and a lower jaw typical of *D. deserti*. It seems obvious that there was a mix-up of the skulls of these two specimens, probably during the process of cleaning. In addition to this, the Gila Bend area does not seem to be a suitable habitat for *D. spectabilis*, and in the same way, Indian Oasis does not seem to be a suitable habitat for *D. deserti*. The card file of the U.S. National Museum, indicates that specimen, No. 229343 ♂, identified as *D. spectabilis*, from Gila Bend, is missing. No. 229343 from Gila Bend is here regarded as a *D. deserti arizonae* and No. 229351 from Indian Oasis as a *D. spectabilis perblandus*.

Specimens examined. A total of 262 specimens from:

ARIZONA. PINAL COUNTY: Florence, 2 (AMNH); 9 mi W Oracle, 3,600 ft, 2 (KU); 5 mi W Oracle, 2 (KU); Oracle, 6 (USNM). PIMA COUNTY: 10 mi N Tucson, 2,800 ft, 3 (USNM); vic. of Fort Lowell, 2 (UCLA); 8 mi E Fort Lowell, 2 (UCLA); Tanque Verde, 1 (KU); Gun-

sight, 2 (USNM); 75 mi W Tucson, 1 (USNM); vic. Tucson, 1 (UI); Tucson, 2 (USNM); Saguaro National Mon., 10 m E Tucson, 2 (UI); Saguaro National Mon., 2 mi S of Park base, 1 (UI); Black Mt., 10 mi S, 2 mi W Tucson, 1 (KU); Copper Mt., Valley of the Ajo, 5 (SDSNH); 1 mi S Copper Mt., Valley of the Ajo, 3 (SDSNH); Ajo Valley, 2,000 ft, 3 mi W Alamo Canyon, 4 (LACM); mouth Alamo Canyon, 2,100 ft, Ajo Mts., 3 (LACM); Baboquivari Mts., T. M. Peter's Ranch, 1 (USNM); 30 mi SE Tucson, 1 (USNM); 5 mi NW Sells, 3 (SDSNH); Sells (airport), 15 (UI); Indian Oasis [=Sells], 6 (USNM); N base Santa Rita Mts., 4,000 ft, 2 (USNM); Gray's Ranch, Sonoita Valley, 1 (SDSNH); Hartt, 23 mi S Tucson, 8 (LACM); Continental (26 mi S Tucson), 2,900 ft, 1 (UCLA); Continental, 1 (USNM); Sabino Canyon, 23.5 mi N, 4 mi E Sásabe, 1 (UI); Sabino Canyon, Baboquivari Mts., 5 (UI); 75 mi SW Tucson, 1 (USNM); 1 mi S Topawa, 2 (UI); 30 mi S Tucson, 4,100 ft, 16 (KU); 14 mi E, 3 mi S Continental, 4,000 ft, 10 (KU); 6 mi E, 5 mi S Continental, 1 (UI); NW Santa Rita Mts., 7 mi S, 8 mi E Continental, 2 (KU); 35 mi S Tucson, Santa Rita Range Reserve Sta., 4,300 ft, Ruelas Sta., 2 (USNM); Santa Rita Exp. Range, NE Station, 2 (UI); 35 mi S Tucson, Santa Rita Exper. Range, 3,900 ft, Climatic Sta., 15 (USNM); 35 mi S Tucson, Santa Rita Range Reserve Sta., 3,800 ft, 3 (USNM); 35 mi S Tucson, Santa Rita Res., 1 (USNM); 35 mi S Tucson, across road from Road Sta., 4,000 ft, 5 (USNM); 35 mi S Tucson, Santa Rita Range Res., Desert Canal, 3,500 ft, 1 (USNM); Santa Rita Grazing Reserve, 3,600 ft, 1 (USNM); Santa Rita Range Reserve, 5½ mi NW Florida Ranger Sta., 3,500 ft, 8 (CAS); Santa Rita Range Res., 4½ mi NW Florida Ranger Sta., 3,500 ft, 11 (CAS); 1¾ mi S, 1 mi W, NE Station, Santa Rita Exp. Range, 1 (UI); W slope Santa Rita Mts., 4,500 ft, 1 (UCLA); E slope Baboquivari Mts., 10 mi N International boundary, 4,000 ft, 1 (UCLA); ½ mi E Arivaca, 3 (UI); Sapo Tank, 1¼ mi S, ¼ mi E Arivaca, 1 (UI); Sapo Tank, 1½ mi S, ¼ mi E Arivaca, 9 (UI); 4 mi N, 1 mi E Sásabe, 1 (UI); La Osa, Altar Valley, 3 (MVZ); La Osa, 7 (USNM). SANTA CRUZ COUNTY: Santa Rita Mts., below Sawmill Cañon, 3,500 ft, 4 (CAS); Tubac, 1 (FMNH); Calabasas, 10 (USNM); 8½ mi N, 2½ mi W Nogales, 1 (KU); 9 mi NE Nogales, Patagonia Mts., 3 (UI); 9 mi ENE Nogales, Patagonia Mts., 10 (UI); 7 mi NW Nogales, Calabasas Canyon, 3 (UI).

SONORA. Pozo de San Emeterio, 8½ mi N Quitovac, 4 (MVZ); Cerro Blanco, 1 (FMNH); Magadalena, 2 (USNM); Llano, 2 (USNM); 20 mi S Santa Ana, 2,600± ft, 23 (MVZ).

Additional records. ARIZONA. PINAL COUNTY: between Florence and Tucson, along Hwy. 80, 1 (CM, Doutt, 1934:262; recorded as *D. s.*

spectabilis) : 6 mi NW Oracle Junction, 3 (CM, Cockrum, 1960:144) ; 2 mi N, 5 mi W Oracle, 1 (UA) ; 27 mi N, 4 mi E Tucson, 1 (UA) ; few miles E Oracle (Gibbs, 1955:463) ; 1 mi S Oracle, 1 (UA, Lange, 1960: 447). PIMA COUNTY: Ajo (Vorhies and Taylor, 1922:9; recorded as *D. s. spectabilis*) ; 3 mi E Tucson, 1 (UA, Cockrum, 1960:144) ; Black Mt., 10 mi SW Tucson, 1 (UA) ; 30 mi S Ajo, Organ Pipe Cactus National Monument, 2 (CM, Cockrum, 1960:144) ; Santa Rita R. S., Melendreth Wash, 3,700 ft, 1 (UA, Cockrum, 1960:144) ; vic. Copper Mt. (Huey, 1942:361) ; about 1 mi NE Gray's Ranch (Huey, 1942:361) ; Clark Ranch, 4 mi E Arivaca, 3,890 ft, 1 (UA, Cockrum, 1960:144) ; near Sásabe, 2 (MSU). SANTA CRUZ COUNTY: ½ mi S Calabasas, 8 (UA, Cockrum, 1960:144).

SONORA. 2 mi S Sásabe, 2 (Dice and Blossom, 1937:30) ; Noria (UCLA, Burt, 1938:46) ; Ebano (Alvarez, 1960:406).

Dipodomys spectabilis intermedius Nader

Dipodomys spectabilis intermedius Nader, Proc. Biol. Soc. Washington, 78 (5) :50, 21 July 1965, original description.

Type. Female, adult, skin and skull; No. 82782, Museum of Vertebrate Zoology, University of California; from 16.7 miles southwest of Bámori, 1,900± feet, Sonora, México; obtained by Seth B. Benson, 25 April 1938, original number 5301.

Range. West central Sonora.

Known at present from the vicinity of Querobabi on the north, southward to Carbo and westward to a locality about 17 miles southwest of Bámori. Limits of the range of this subspecies are not well known.

Diagnosis.

Size: Small; adult total length 318.5 to 325.0 mm; tail length 184.9 to 188.8 mm; ear length 16.16 mm; white tip of tail short, 20.0 to 21.0 mm; weight 98.8 to 106.1 grams.

Color: Upper parts Light Ochraceous-Buff mixed with Pinkish Buff and thinly mixed with black-tipped hairs; sides with more evident Pinkish Buff; arietiform markings dusky; plantar stripes light brown; tuft of hairs at base of tail ventrally grayish; dorsal and ventral tail stripes darkish; subterminal band of tail blackish.

Skull: Small-sized; greatest length 43.0 to 43.2 mm; basal length 31.0 mm; breadth across maxillary arches small; posterolateral edge of

maxillary arches slightly flared; lacrimal not too uniform in shape; rostrum narrow; auditory bullae small; greatest breadth across bullae 27.0 to 27.7 mm; supraoccipital and interparietal narrow; least supraoccipital breadth 1.7 to 2.0 mm; breadth across exoccipitals narrow; external openings of auditory meati oval; incisors usually small; mandibular length small, 17.9 to 18.0 mm. Also see Table 6.

Comparisons. For comparison with *Dipodomys spectabilis perblandus,* see account of that subspecies (pp. 36 ff.).

Remarks. Typical *Dipodomys spectabilis intermedius* is characterized by small size in such features as total length, skull, auditory bullae, and mandible, Pinkish Buff on sides, and a short white tail tip.

This subspecies intergrades with *D. s. perblandus* in central Sonora. One adult from 5 mi W Querobabi, which is referred to *D. s. intermedius,* has some cranial characters similar to those of *D. s. perblandus.*

Variation within the range of *D. s. intermedius* includes the following: One adult male from 45 mi N Hermosillo has the breadth across the maxillary arches and the greatest breadth across the bullae slightly larger than typical. Two adult paratypes have the least width of the supraoccipital approaching that of *D. s. perblandus.*

Specimens examined. A total of 18 specimens from:

SONORA. 16.7 mi SW Bámori, 1,900± ft, 9 (MVZ); 5 mi W Querobabi, 4 (KU); 45 mi N Hermosillo, 2,100± ft, 5 (MVZ).

Dipodomys spectabilis baileyi **Goldman**

Dipodomys spectabilis baileyi Goldman, Proc. Biol. Soc. Washington, 36:140, 1 May 1923, original description.

Dipodomys spectabilis clarencei Goldman, J. Washington Acad. Sci., 23:467, 15 October 1933. Type: Male, adult, skin and skull; No. 158824, U. S. Biological Surveys Collection; from Blanco, San Juan County, New Mexico; obtained by Clarence Birdseye, 19 November 1908, original number 443.

Type. Male, young adult, skin and skull; No. 97185, U. S. Biological Surveys Collection; from 40 miles west of Roswell, Lincoln County (not Chaves County, Hall and Kelson, 1959:528), New Mexico; collected by Vernon Bailey, 13 June 1899, original number 6961.

Range. Northeastern Arizona; northwestern, central, and southeastern New Mexico; western Texas.

More specifically, in northeastern Arizona, from the western side of the Chinle Valley, to about 25 miles southwest of Chinle, Apache County. In northwestern New Mexico, from the San Juan River Valley, to Blanco and Cañon Largo, San Juan County, to the vicinity of Gallup, McKinley County, to San Agustin Plains, Catron County, to Rio Alamosa Valley, Socorro County, to the vicinity of Las Palomas, Sierra County, and the eastern valley of the Rio Grande. In eastern New Mexico, from the Jemez River Valley, Sandoval County, to the vicinity of Santa Fe, Santa Fe County, to the vicinity of Santa Rosa, Guadalupe County, and along the eastern valley of the Pecos River to the vicinity of Floyd, Roosevelt County, to the vicinity of Caprock, Chaves County, south to southeastern New Mexico. In western Texas, from the eastern valley of the Rio Grande, to the vicinity of Marfa, Presidio County, and from the vicinity of Andrews, Andrews County, to the vicinity of Tarzan, Martin County, south to the vicinity of Midland, Midland County, to Odessa, Ector County, and the vicinity of Iraan, Pecos County. Limits of range are fairly well known. This race may be found in southeastern Utah and southwestern Colorado. Also, it may occur south of the known range in western Texas.

Diagnosis.

Size: Large; adult total length 351.0 to 374.0 mm; tail length 207.0 to 224.0 mm; body length 146.4 to 156.0 mm; hind foot length 54.6 to 57.0 mm.

Color: Upper parts, in general, Light Ochraceous-Buff and occasionally Pinkish Buff, purest on sides and shoulders, moderately mixed with black-tipped hairs, especially over top of head and back; arietiform markings blackish; anterior ear fold blackish; large spot behind ankle blackish; plantar stripe brownish black to black; tuft of hairs at base of tail ventrally blackish; dorsal and ventral tail stripes blackish, inconspicuously mixed with gray; subterminal band of tail black.

Skull: Large and massive; greatest length 46.3 to 47.9 mm; basal length 34.2 to 35.6 mm; maxillary arch heavy; dorsal anteromedial edge of maxillary arch projecting farther forward along premaxilla; maxillary arch not sharply slanted posteriorly, and its posterolateral edge not flared out; breadth across maxillary arches 26.7 to 28.0 mm; lacrimal wide and uniform; auditory bullae large; greatest breadth across bullae 29.8 to 30.5 mm; opening of external auditory meatus large and oval shaped; pterygoid foramen large; mandibular length 20.1 to 21.4 mm; incisors heavy. Also see Table 6.

Comparisons. For comparisons with *Dipodomys spectabilis spectabilis,* see account of that subspecies (pp. 30 ff.).

Remarks. Typical *Dipodomys spectabilis baileyi* is characterized by an Ochraceous-Buff color and occasionally a Pinkish Buff color, moderately mixed with black-tipped hairs and with the dorsal and ventral tail stripes grayish black. Most external and cranial measurements are the largest for the species. *D. s. baileyi* has large bullae, heavy maxillary arches, and heavy teeth.

Goldman (1933:467) regarded the populations in northwestern New Mexico as a distinct subspecies (*D. s. clarencei*). In the 20 measurements studied in this report, none appeared to be distinctive in these northwestern populations. In comparing *D. s. clarencei* with *D. s. baileyi,* Goldman (1933) stated that the former has a similar color, but less distinct arietiform markings and the upper surface of the muzzle behind the nasal pad is more extensively white. No real difference was found in the distinctness of the arietiform markings between specimens from northwestern New Mexico and those from central and southeastern New Mexico. Also, the white spot behind the nasal pad does not seem to be a good character on which to base distinctions, since it is not present in the majority of the specimens from northwestern New Mexico, and it is present in many specimens from central and southeastern New Mexico. With regard to cranial characters, Goldman (1933) stated that *D. s. clarencei* is smaller than *D. s. baileyi,* with a relatively broader frontal region, with more strongly developed external angles on the maxillary arches (tending to form more strongly projecting hooks), and with narrower incisors. The hook development of the maxillary arches is not a distinctive character for the northwestern populations, because it is present in many specimens throughout the range of *D. s. baileyi.* No real differences were detectable in the width of the incisors or in the least interorbital breadth (an indication of frontal width) in a comparison of northwestern populations and the rest of *D. s. baileyi.* In a scatter diagram (Fig. 7) using greatest breadth across the bullae and greatest length of the skull, it was not possible to show any difference in the size of the skull between the two populations. Thus *D. s. clarencei* is regarded here as consubspecific with *D. s. baileyi.*

Dipodomys spectabilis baileyi intergrades with *D. s. spectabilis* in a wide zone along the Rio Grande in south central New Mexico and western Texas (see also *Remarks* under *D. s. spectabilis,* p. 32). Adults from Magdalena and from the vicinity of Socorro, Socorro County,

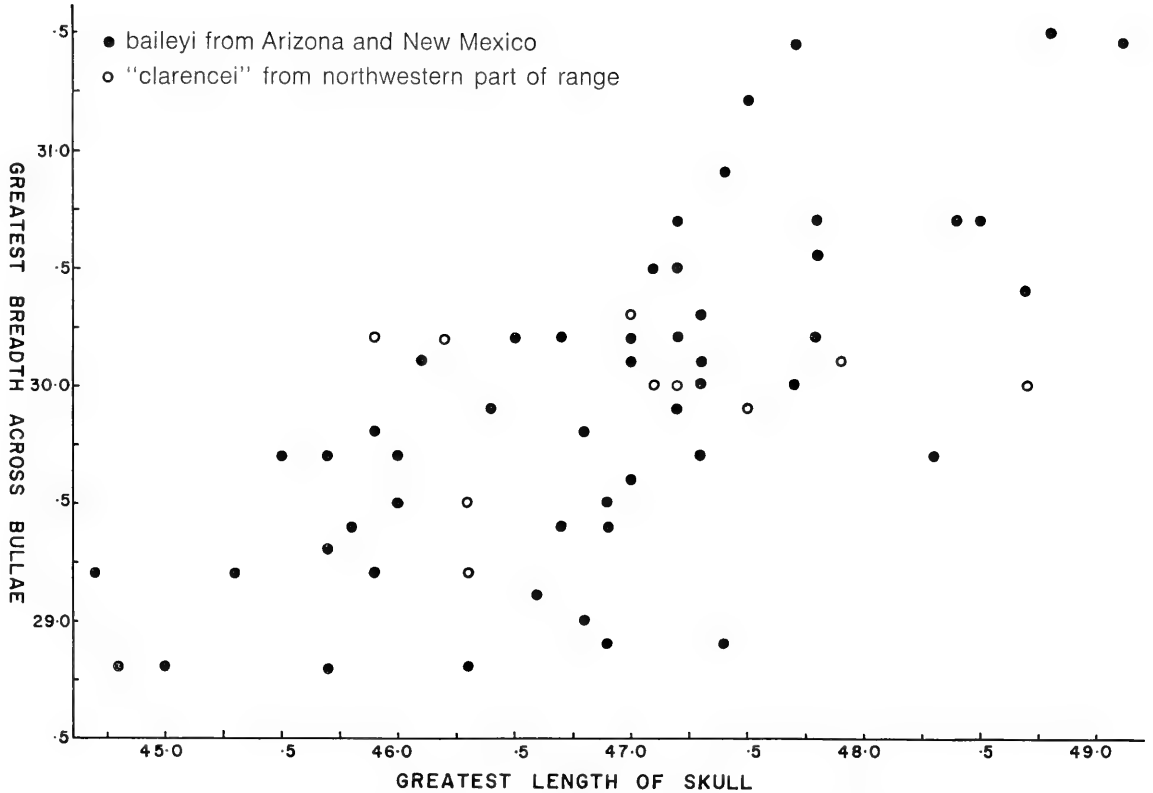


Fig. 7. Scatter diagram showing comparison between greatest breadth across the bullae and greatest length of the skull of all examined adult *D. s. baileyi* from Arizona and New Mexico, and *D. s. "clarencei"* from northwestern part of range.

New Mexico, have narrower rostra than typical *D. s. baileyi*. The skull of the adult from Parker Lake, east Organ Mountains, Dona Ana County, is narrow across the maxillary arches and in this respect is similar to *D. s. spectabilis*. Many specimens from several localities in western Texas are smaller in several external and cranial measurements than typical *D. s. baileyi*, to which they are referred herein, but are within the range of *D. s. spectabilis*.

Compared with typical *D. s. baileyi*, adults from the vicinity of Chinle, Apache County, Arizona, and from Fruitland, San Juan County, and from Santa Fe, Santa Fe County, New Mexico, are smaller in some cranial characters. Some adults from northwestern New Mexico have shorter tails and smaller hind feet. Others from central New Mexico are smaller in rostral depth and in bullar depth. These variations are not uniform, and the populations are not well marked for taxonomic recognition.

Three specimens in the UNM collection, Nos. 14870 ♂, 14871 ♀, and 14872 ♂, from 15 mi W, 7 mi N Jal, are new records of this subspecies for Lea County, New Mexico. Also three specimens in the LACM collection, Nos. 4124 ♂ skin only, 2125 ♂, and 2126 ♂, from 20 mi N Pecos, Loving County, represent new county records in Texas.

Specimens examined. A total of 211 specimens from:

ARIZONA. APACHE COUNTY: 8 mi S Chin Lee [now Chinle], 5,500 ft, 1 (USNM).

NEW MEXICO. SAN JUAN COUNTY: Fruitland, 4 (USNM); Blanco, 3 (USNM); 7 mi S, 6 mi W Bloomfield, T 27 N-R 12 W, Sec. 4, 2 (UNM); 1 mi E, 9 mi S Bloomfield, T 27 N-R 11 W, Sec. 11, 1 (UNM); Gallegos Store, 10 mi S, 7 mi W Bloomfield, 1 (UNM); Chaco Canyon National Mon., 6,400 ft, 4 (MVZ); Chaco Canyon, 6,400 ft, 1 (USNM). MCKINLEY COUNTY: 15 mi NW Gallup, 2 (USNM). SANDOVAL COUNTY: Jemez River Valley, 1 (AMNH); 12 mi NW Alameda, 5,500 ft, 2 (MVZ). VALENCIA COUNTY: Juan Tafoya, 1 (USNM); 10 mi SE Belen, 5,000 ft, 1 (UNM). BERNALLIO COUNTY: 6 mi E, 1 mi N Alameda, 1 (UNM); Juan Tabo Road, 2 mi W recreational area, 1 (UNM); Mesa, 5 mi W Albuquerque, 1 (UNM); Albuquerque, 3 (USNM). CATRON COUNTY: Mayberry Ranch, 75 mi W Magdalena, 6,600 ft [skin tag: Socorro Co.], 1 (USNM). SOCORRO COUNTY: 10.5 mi W, 4.7 mi N Bernardo, 1 (UNM); Juniper zone, below Lardon, T 3N, R 3W, Sec. 36, 1 (UNM); ½ mi S, 2 mi W Bernardo, 1 (UNM); Bear Spring Mts., 3 (USNM); Riley, 1 (USNM); 9 mi N Lemitar, Rio Salado, 1 (UNM); Gallina Mts., 2 (USNM); 1½ mi N, 5 mi W Magdalena, 1 (KU); Magdalena, 2 (USNM);

Socorro, 5 (USNM); Range, 2 mi SW Socorro, 4,700 ft, 2 (MVZ); 4 mi S, 3 mi W Socorro, 8 (UNM); 15 mi W, 11 mi S Magdalena, San Augustin [=Agustin] Plains, 1 (UNM); Big Rosa Cañon, 1 (UNM); Big Pigeon Ranch, San Mates [Mateo] Mts., 1 (USNM); Rio Alamosa, 15 mi N Ajo Caliente, 6,900 ft, 5 (USNM); 7.5 mi E Springtime Canyon, San Mateo Mts., 1 (UNM); Nogal Canyon, 28 mi S, 17 mi W San Antonio, 1 (UNM). SIERRA COUNTY: 5½ mi E, 1 mi N Engle, 2 (UNM). DONA ANA COUNTY: 25 mi N Las Cruces, 1 (UNM); Las Cruces, on the mesa, 4,000 ft, 1 (USNM); Parker Lake, E Organ Mts., 2 (USNM). SANTA FE COUNTY: 6 mi N of NE corner Santa Fe Municipal Airport, 1 (KU); 5 mi NW Santa Fe, T 17N, R 8W, Sec. 1 and 12, 1 (UI); 1 mi W Santa Fe Municipal Airport, 1 (KU), 1 (UI); Santa Fe Municipal Airport, 6,300 ft, 1 (UI); 8 mi SW Santa Fe, 5 (KU); 11 mi SW Santa Fe, 4 (CAS); 12 mi SW Santa Fe, N border of Airport, 1 (CAS); 15 mi SW Santa Fe, 1 (CAS), T 15N, R 8E, Sec. 34 and 35, 1 (UI); Simmons Ranch, 8 mi SE Golden, 6,500 ft, 1 (MVZ). TORRANCE COUNTY: 3½ mi S, 8½ mi E Cline's Corners, 6,500 ft, 1 (KU); Monzano Mts., E foothills N end, 6 (USNM); 10 mi E, 2 mi S Willard, 1 (UNM); Mesa Jumanes, N portion [34° 25′ N, 106° 05′ W], 2 (USNM). GUADALUPE COUNTY: Santa Rosa, 1 (USNM). DE BACA COUNTY: Alamogordo Reservoir below dam, 9 mi N, 9 mi W Ft. Sumner, 1 (UNM). LINCOLN COUNTY: Ancho, 2 (USNM); French's Ranch, 12 mi NW Carrizzo, 5,400 ft, 1 (MVZ); W edge lava bed [8 mi NW Carrizzo], 1 (UNM); 7 mi W Carrizzo, 1 (UM); Capitan, Flying H Ranch, 6,000 ft, 2 (USNM); 44 mi NW Roswell, 19 (MVZ); 40 mi W Roswell, 1 (USNM); 30 mi W Roswell, 2 (USNM). OTERO COUNTY: 12 mi SW Alamogordo, 3 (SDSNH). CHAVES COUNTY: 35 mi N Roswell, 1 (USNM); 20 mi N Roswell, 3 (USNM); 9.3 mi E, 8.2 mi S Roswell, 1 (UNM). EDDY COUNTY: Carlsbad Cave, 3 (USNM); 6 mi S, 10 mi W White's City, 4,100 ft, 1 (KU). LEA COUNTY: 15 mi W, 7 mi N Jal, 3 (UNM).

TEXAS. EL PASO COUNTY: El Paso, Flats E Franklin Mts., 1 (USNM); 12 mi E, 1 mi S City Hall, El Paso, 4,000 ft, 1 (KU); Fabens, San Felipe Arroyo, 1 (UNM). HUDSPETH COUNTY: Sierra Blanca, 3 (USNM). CULBERSON COUNTY: 35 mi N Van Horn, 3,600 ft, 1 (TCWC); 11 mi N Kent, 4,500 ft, 2 (TCWC); 6 mi N Kent, 4,000 ft, 3 (TCWC); 16 mi E Van Horn, 3,000 ft, 1 (TCWC); Kent, 1 (USNM); 16 mi SE Van Horn, 4,100 ft, 1 (TCWC). JEFF DAVIS COUNTY: Fort Davis, 1 (UM); Valentine, 3 (USNM); 14½ mi SW Fort Davis, 2 (UM). PRESIDIO COUNTY: 10 mi NE Marfa, 5 (UM); Marfa, 4 (UI), 1 (UM). LOVING COUNTY: 20 mi N Pecos, 3 (LACM). REEVES COUNTY: Toyah, 2 (USNM); 20 mi S Pecos, 2,900 ft, 1 (KU); 5 mi E Toyahvale, 2 (USNM). WARD COUNTY:

Monahans, 16 (USNM); Grand Falls [=Grandfalls], 8 mi SW Castle Mts., 1 (USNM). PECOS COUNTY: 20 mi E Adams [about 5 mi NW Iraan], 1 (USNM). ANDREWS COUNTY: 14 mi S Andrews, Sam Arnett Ranch, 4 (UM). ECTOR COUNTY: 3 mi NE Penwell, 1 (UI). CRANE COUNTY: Castle Mts., 7 mi SW Castle Gap, 1 (USNM).

Additional records. ARIZONA. COCONINO COUNTY: 5 mi E Rainbow Lodge, 6,000 ft. (Hoffmeister, 1977:150) not plotted on Fig. 5. APACHE COUNTY: 10 to 25 mi SW Chinle (Goldman, 1933:467).

NEW MEXICO. (All from Bailey, 1931:259–260, unless otherwise noted), SAN JUAN COUNTY: near Bloomfield, N side San Juan River; Largo Canyon [=Cañon Largo]; Blanco Canyon; San Juan Valley, E base Chuska Mts.; Kimbetoh Valley [=Kinebeto Wash]; Escavada Valley [=Escarbada Wash]. MCKINLEY COUNTY: N Hosta Butte Mts.; W Gallup. SANDOVAL COUNTY: Valley of Salado Creek, E and N Cabezon; on the mesa, 6 mi E Algodones. VALENCIA COUNTY: Cubero; Laguna; 15 mi SW Acoma. BERNALLIO COUNTY: 8 mi NNW Albuquerque (Ivey, 1957:496); on the mesa, 3 mi E Albuquerque; W base Sandia Mts., E Albuquerque, 6,000 ft (Vorhies and Taylor, 1922:8); 15 mi WSW Albuquerque, 3 (Ivey, 1957:496). CATRON COUNTY: foothills of Datil Mts.; edge of San Augustin [=Agustin] Plain. SOCORRO COUNTY: foothills of Gallina Mts., Plains near Magdalena; 3 or 4 mi NW Socorro. SIERRA COUNTY: Jordana Valley; on the mesas about Cuchillo; on the mesas near Las Palomas. DONA ANA COUNTY: between Garfield and Rincon; 8 mi E Mesilla Park, 4,800 ft; base Organ Mts., 5,200 ft; E base Franklin Mts. GUADALUPE COUNTY: 8 or 10 mi N Santa Rosa. DE BACA COUNTY: N Fort Sumner. LINCOLN COUNTY: NW base Jicarillo Mts., 2; 50 mi NW Roswell; on the Malpais, W Oscuro (Blair, 1941: 223). OTERO COUNTY: E border Tularosa Valley; S end Tularosa Valley, near Jarilla. CHAVES COUNTY: 15 mi N Roswell; E side Pecos River, 15 mi NE Roswell (Vorhies and Taylor, 1922:9); 12 mi NW Roswell; 4 mi W Caprock, 2 (Ramsey and Carley, 1970:351); 3 mi W and 1 mi N Caprock, 1 (Judd and Schmidly, 1969:382). EDDY COUNTY: along railroad, between Roswell and Carlsbad; foot Guadalupe Mts., 30 mi W Carlsbad; Carlsbad (Vorhies and Taylor, 1922:9); Pecos Valley, 30 mi E Carlsbad. ROOSEVELT COUNTY: 9 mi S and 1 mi W Tolar (Best, 1972:201); 4 mi W Floyd (Best, 1972:202).

TEXAS. EL PASO COUNTY: 10 mi N El Paso, E base Franklin Mts., 1 (Bailey, 1905:147); lower edge Franklin Mts. (Vorhies and Taylor 1922:9). CULBERSON COUNTY: Van Horn (Bailey, 1905). JEFF DAVIS COUNTY: 16 mi NE Ft. Davis, 1 (TCWC); 4 mi SW Fort Davis, 5,000 ft,

1 (UM, Blair, 1940:29); 12 to 14 mi SW Fort Davis, 11 (UM, Blair, 1940:29). PRESIDIO COUNTY: 11 mi W Valentine, 3 (TMM); about 7 mi NE Marfa, 5 (UM, Blair, 1940:29); 2 mi S Paisano, 3 (TCWC). REEVES COUNTY: Pecos (Bailey, 1905): Toyahvale (Bailey, 1905). ANDREW COUNTY: 25 mi NE Kermit, 1 (Packard and Judd, 1968:537). WINKLER COUNTY: 7 mi SW Kermit, 3 (Packard and Judd, 1968:537). PECOS COUNTY: Adams [about 5 mi NNW Bakersfield (Bailey, 1905)]. ECTOR COUNTY: Odessa (Bailey, 1905). MARTIN COUNTY: all from Ramsey and Carley (1970:351): Midland Water Station (7 mi S Patricia); 7 mi W Tarzan, 2; 12 mi S Flower Grove, 2; 1 mi S and 18 mi W Stanton, 3. MIDLAND COUNTY: 8 mi W and 5 mi N Midland, 13 (Ramsey and Carley, 1970:351).

Dipodomys spectabilis zygomaticus Goldman

Dipodomys spectabilis zygomaticus Goldman, Proc. Biol. Soc. Washington, 34:140, 1 May 1923, original description.
Dipodomys nelsoni: Baker and Greer, 1962:100 (part).

Type. Male, young adult, skin and skull; No. 96432, U. S. Biological Surveys Collection; from Parral [=Hidalgo del Parral], southern Chihuahua, México; obtained by E. A. Goldman, 17 September 1898, original number 13030.

Range. South central Chihuahua and north central Durango.

More specifically, west in Chihuahua from the vicinity of Hidalgo del Parral, east to the vicinity of Búfalo and Salaíces. North from the vicinity of Ciudad Camargo and south of the Río Conchos in Chihuahua, south to north central Durango around the vicinity of La Resolana. Limits of the range are well known only on the eastern side; more collecting is still needed. Limits in the other directions are poorly known and need to be clarified. More collecting west of the present known range may reveal *D. s. zygomaticus* to be present as far west as the valley east of the San Juan River. Also future collecting may show a wider range in northwestern and north-central Durango and may bring *D. s. zygomaticus* in contact with *D. s. nelsoni.*

Diagnosis.

Size: Medium; adult body length 135.7 to 140.0 mm; white tip of tail medium 20.0 to 28.0 mm.

Color: In general, Light Ochraceous-Buff, purest on sides, rather heavily mixed with black-tipped hairs on dorsum, especially over top

of head, back, and rump; arietiform markings black; anterior ear fold black; large spot behind ankle black; plantar stripes brownish or dusky; tuft of hairs at base of tail ventrally black; dorsal and ventral tail stripes gray mixed with black; subterminal band of tail black.

Skull: Medium-sized; length of nasals 16.0 to 16.3 mm; maxillary arch heavy; posterolateral edge of maxillary arch usually flared out; breadth across maxillary arches 25.9 to 26.9 mm; least interorbital breadth 16.0 to 16.8 mm; auditory bullae usually expanded in front of meatus; jugals usually divergent posteriorly; pterygoid foramen usually round. Also see Table 6.

Comparisons. Compared with *Dipodomys spectabilis cratodon, D. s. zygomaticus* differs as follows: Total length greater and tail usually longer; upper parts more heavily mixed with black-tipped hairs; arietiform markings usually darker; skull shorter as indicated by greatest length; maxillary arch slightly less heavy and less angled with long axis of skull; nasals longer; region of premaxillaries and nasals anterior to maxillary arch narrower; interorbitally wider; least supraoccipital breadth usually less; incisors narrower and less massive; jugals usually more divergent posteriorly; auditory bullae usually more inflated anterior to the opening of the external auditory meatus.

Compared with *Dipodomys spectabilis nelsoni, D. s. zygomaticus* differs as follows: Slightly larger in all external measurements; usually with longer white tip of tail, but relatively same length; usually with more ochraceous buff color; more heavily mixed with black-tipped hairs; darker arietiform markings; skull usually larger in all measurements; maxillary arches relatively as well as actually heavier; auditory bullae relatively as well as actually larger; jugals usually divergent posteriorly; auditory bullae usually expanded anterior to opening of external auditory meatus; upper incisors usually wider; mandible usually longer.

For comparison with *Dipodomys spectabilis spectabilis,* see account of that subspecies (pp. 30 ff.).

Remarks. Typical *Dipodomys spectabilis zyogmaticus* is characterized by a Light Ochraceous-Buff color, rather heavily mixed with black-tipped hairs. The auditory bullae are usually expanded in front of the meatus, and the jugals are usually divergent posteriorly.

Goldman (1923:141) in his diagnosis of *D. s. zygomaticus* stated that the skull is similar to that of *D. s. spectabilis,* but "broader especially posteriorly between outer sides of audital bullae." In comparing the averages of the greatest breadth across the bullae of this subspecies

with those of *D. s. spectabilis*, no significant difference was found. Only the specimens from the type-locality and some specimens from 2 mi W Parral and 5 mi E Parral are broad across the bullae. In all other localities where this subspecies is found, the average width across the auditory bullae is within the range of *D. s. spectabilis*. Goldman apparently based his diagnosis of *D. s. zygomaticus* on the four specimens then available to him from the type-locality. In a scatter diagram based on nasal length and least interorbital breadth, it was possible to separate 96% of all adults examined of *D. s. zygomaticus* from 86.6% of all adults examined of Chihuahuan *D. s. spectabilis* (see Fig. 8, and also comparisons with *D. s. spectabilis*).

D. s. zygomaticus in its present range is far removed geographically from *D. s. cratodon* to the southeast. The species *spectabilis* apparently has been present at one time or another throughout the elevated plains of central Durango and west central Zacatecas.

The contact zone between *D. s. zygomaticus* and *D. s. spectabilis* is not well defined; however, specimens from the northern part of the range of *D. s. zygomaticus* in Chihuahua show intergradation with *D. s. spectabilis*. It is believed that the Río Conchos is an effective barrier between these two subspecies. Specimens from Santa Rosalia and from 2 mi SE Boquilla, which are referred here to *D. s. zygomaticus*, may be regarded as intergrades.

Dipodomys spectabilis zygomaticus intergrades with *D. s. nelsoni* in the vicinity of Búfalo and Salaíces in south central Chihuahua, and in the vicinity of La Resolana in north central Durango. Future collecting may reveal a greater degree of intergradation in this area. For a discussion of the zone of intergradation and the degree of overlap between the measurements studied, see *Remarks* under *D. s. nelsoni* (pp. 57–58).

Three specimens in the MSU collection, Nos. 4909–11, from 12 mi NW La Resolana, Durango, were assigned by Baker and Greer (1962: 101) to *D. nelsoni*. Two of these specimens (Nos. 4909–10) were examined (No. 4911 was deposited at the Department of Game, Mexico City, México), and are referred here to *D. s. zygomaticus*. One of the specimens (No. 4909 ♂), seems closer in its measurements to *D. s. nelsoni* because it is a subadult. The other specimen, No. 4910, is an adult female and its measurements are within the range of *D. s. zygomaticus*, although smaller than average.

One adult specimen from 4½ mi ESE Boquilla, Chihuahua, is typical of *D. s. zygomaticus* in coloration, but with a larger than typical skull and with incisors as heavy as those of *D. s. cratodon*. Also it has

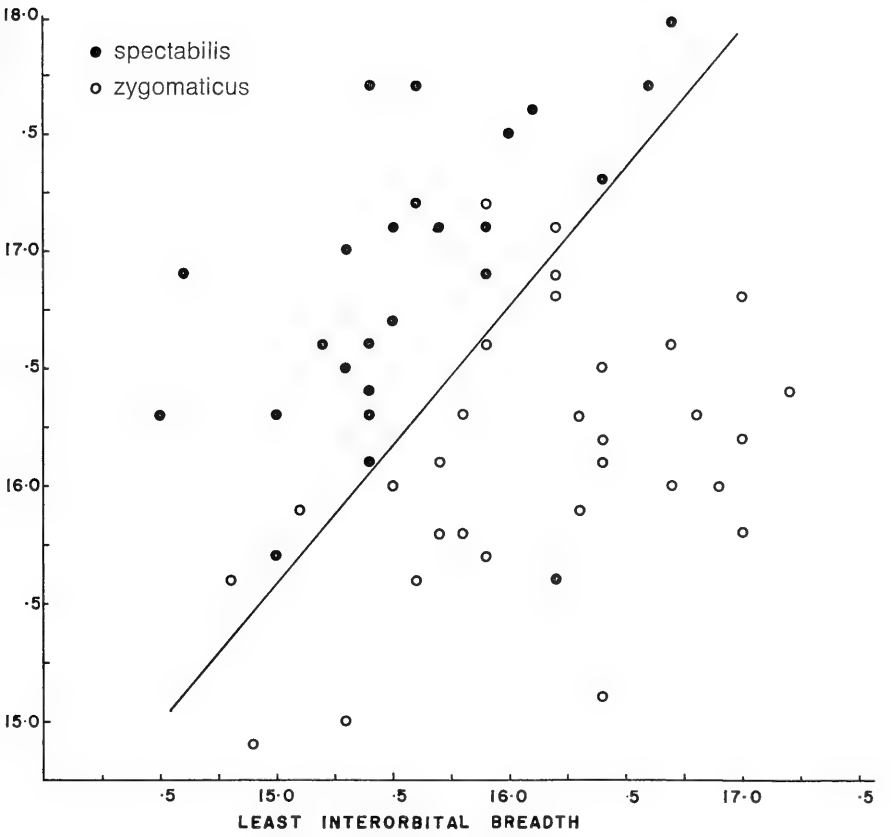


Fig. 8. Comparison between length of nasals and least interorbital breadth of all examined adult *D. s. zygomaticus* (except those from zone of intergradation with *D. s. nelsoni*), and all examined adult Chihuahuan *D. s. spectabilis*. The equation of the discriminant function line which best separates these populations is approximately $y = -.4 + 1.\emptyset\, x$ where y is the length of the nasals and x is the interorbital breadth.

wide nasals and large bullae, but the bullae are not expanded anterior to the opening of the external auditory meatus. Jugals in this specimen are not divergent.

Specimens examined. A total of 73 specimens from:

CHIHUAHUA. Santa Rosalia [=Ciudad Camargo], 4 (USNM); 2 mi SE Boquillas [=Boquilla], 4,700 ft, 3 (KU); 4.5 mi ESE Boquillas, 4,700 ft, 1 (KU); 7.5 mi ESE Boquillas, 4,700 ft, 1 (KU); 9.5 mi ESE Boquillas, 4,700 ft, 2 (KU); 10.5 mi ESE Boquillas, 4,700 ft, 3 (KU); 13.5 mi ESE Boquillas, 4,700 ft, 4 (KU); 14.5 mi ESE Boquillas, 4,700 ft [about 3 mi NW Búfalo], 1 (KU); 15 mi ESE Boquillas, 4,700 ft [about 2.5 mi NW Búfalo], 12 (KU); 1 mi W Búfalo, 4,700 ft, 1 (KU); 1 mi S Búfalo, 4,700 ft, 1 (KU); 29 mi N, 12 mi E Parral [=Hidalgo del Parral], 1 (KU); 22 mi N, 8 mi E Parral, 1 (KU); 15 mi N, 5 mi E Parral, 1 (KU); 12 mi N, 2 mi E Parral, 1 (KU); 19.5 mi WSW Jiménez, 5,000 ft, 3 (KU); 21.5 mi WSW Jiménez, 4,800 ft, 1 (KU); 6 mi N Parral, 1 (KU); 5 mi N Parral, 1 (KU); 3 mi NNW Hidalgo del Parral, 2 (MVZ); 2 mi W Parral, 6,200 ft, 9 (MVZ); Parral, 4 (USNM); 5 mi E Parral, 5,700 ft, 9 (KU); 21.5 mi E Parral, 5,200 ft, 2 (KU); 23 mi E Parral, 1 (KU); 10 mi SE Parral, 6,000± ft, 1 (KU).

DURANGO. 12 mi NW La Resolana, 6,000 ft, 2 (MSU).

Additional records. CHIHUAHUA. 18 mi SSE Villa Matamoros, 5,700 ft (Baker and Greer, 1962:101).

DURANGO. 12 mi SE Las Nieves, 5,750 ft (Baker and Greer, 1962: 101).

Dipodomys spectabilis cratodon Merriam

Dipodomys spectabilis cratodon Merriam, Proc. Biol. Soc. Washington, 20:75, 22 July 1907, original description.

Type. Male, young adult, skin and skull; No. 78953, U. S. Biological Surveys Collection; from Chicalote, Aguas Calientes [now Aguascalientes], México; obtained by E. W. Nelson and E. A. Goldman, 2 July 1896, original number 9734.

Range. East-central Zacatecas, northeastern Aguascalientes, and western San Luis Potosí.

More specifically, west from Cañitas in central Zacatecas to Chicalote in central Aguascalientes, east to vicinity of Herradura in western San Luis Potosí and to Jesús María, the southeasternmost known rec-

ord in San Luis Potosí. Limits of range not well known; future collecting may reveal that this subspecies covers most or all of central Zacatecas and may also occur in east central Durango, southeastern Aguascalientes, northeastern Jalisco, northern Guanajuato, and even in northwestern Queretaro.

Diagnosis.

Size: Medium; adult total length 326.5 to 337.0 mm; tail usually short.

Color: In general, Light Ochraceous-Buff, thinly mixed with black-tipped hairs on dorsum, purest on sides; arietiform markings usually dusky; anterior ear fold black; large spot behind ankle dusky to gray; plantar stripe dark brown to brown with lighter shade on ventral side of toes; tuft of hairs at base of tail ventrally dusky; dorsal and ventral tail stripes dusky mixed with gray; subterminal band of tail blackish.

Skull: Medium-sized, massive and squarish; greatest length 44.0 to 45.2 mm; length of nasals 15.5 to 16.0 mm; posterolateral edge of maxillary arch usually flared out; maxillary arch usually forms an almost right angle with long axis of skull; region of premaxillaries and nasals immediately anterior to maxillary arch wide; least interorbital breadth 15.5 to 16.0 mm; interparietal and supraoccipital usually narrow; least supraoccipital breadth 1.0 to 1.5 mm; incisors broad and heavy; pterygoid foramen usually round; auditory bullae large; opening of external auditory meatus usually oval. Also see Table 6.

Comparisons. Compared with *Dipodomys spectabilis nelsoni, D. s. cratodon* differs in the following: Total length and hind foot longer; color more buffy and darker; arietiform markings and subterminal band of tail darker; skull larger and heavier; maxillary arches heavier; nasals longer; interorbital breadth wider; incisors heavier; molariform teeth larger; auditory bullae larger; external opening of auditory meatus larger and more oval; pterygoid foramen rounder; mandible longer and heavier.

For comparison with *Dipodomys spectabilis zygomaticus,* see account of that subspecies (p. 49).

Remarks. Typical *Dipodomys spectabilis cratodon* is characterized by a medium-sized, squarish skull, wide rostrum immediately anterior to the maxillary arches, heavy incisors, and narrow supraoccipital.

The present known range of *D. s. cratodon* is far removed from that of *D. s. zygomaticus,* which is the closest to it morphologically. There

is no known evidence that these two subspecies were in contact at any time, although it is possible that there was a contact zone in central Durango. Also, there is no contact at the present time with *D. s. nelsoni*, but future collecting may show a secondary zone of intergradation in southeastern Durango, in north central Zacatecas, or in central San Luis Potosí.

Alvarez (1960:408) assigned a specimen or specimens (no number is given) from 3 mi N Lulú, Zacatecas, to this subspecies. Although I did not examine the material that Alvarez (1960) used in support of his statement that the range of *D. s. cratodon* covers all of Zacatecas, I believe it is most probable that specimens from near Lulú are *D. s. nelsoni*. Four of a series of five specimens in the MVZ collection (the fifth was deposited at the Dirección General de Caza in México), from the same aforementioned locality, were examined and all were typical of *D. s. nelsoni*.

Merriam (1907:75), in his original description of this form, stated that the skull is the largest of the genus, deep vertically, and with a broad rostrum. It was found that averages of the greatest length are smaller than in *D. s. zygomaticus*, but the basal length, breadth across the maxillary arches, and greatest breadth across the bullae are about the same. However, *D. s. baileyi* is the largest in all these measurements. Average bullar depth of *D. s. cratodon* is slightly larger than that of *D. s. zygomaticus* but is smaller than in *D. s. baileyi*. Average rostral width is slightly smaller and average rostral depth is smaller than for *D. s. baileyi*. If Merriam (1907) is referring to the part of the skull immediately anterior to the maxillary arches as the rostrum, then it is true that this region is broader in *D. s. cratodon* than in any other subspecies of *D. spectabilis*.

It has been observed that kangaroo rats in central Zacatecas bear some resemblance to *D. s. zygomaticus* and/or *D. s. nelsoni*. One adult from Cañitas compared with typical *D. s. cratodon* has some external and cranial characters to suggest *D. s. zygomaticus*. In some skull characters, specimens from central Zacatecas are smaller. It is hard to say whether these specimens are closer to *D. s. zygomaticus* or *D. s. nelsoni*, because there is no known contact zone between *D. s. cratodon* and either of these two subspecies. The closest recorded locality is that for a specimen of *D. s. nelsoni*, 10 mi SW Yerbanís, 6,200 ft, Durango (Baker and Greer, 1962:100).

Specimens from southeastern Zacatecas and northwestern San Luis Potosí are smaller in many characters than typical *D. s. cratodon*. The

difference is slight and irregular and does not seem to be taxonomically significant. Dalquest (1953:118) made a similar observation about the specimens that he had examined from western San Luis Potosí. The small size of specimens from this part of the range of *D. s. cratodon* in Zacatecas and San Luis Potosí may suggest intergradation with *D. s. nelsoni*. Specimens from southwestern San Luis Potosí are more typical of *D. s. cratodon* although some have darker arietiform markings and some specimens from Jesús María are smaller in some characters.

The type-specimens and topotypes have narrower ventral tail stripes, smaller pterygoid foramina, and the maxillary arches of one young adult male (USNM No. 80354) slant more posteriorly than in other specimens assigned to this taxon.

The interparietal bone in this subspecies is either absent or fused with the supraoccipital in 47.5% of all the specimens examined. This is a much higher percentage than in any other subspecies of *D. s. spectabilis*.

Specimens reported on in this study show a considerable extension of the present known range of this subspecies (Hall and Kelson, 1959: 528). Specimens from Cañitas, Zacatecas, represent a northwestern extension of about 50 miles in central Zacatecas and specimens from Jesús María, San Luis Potosí, represent a southeastern extension of about 70 miles in southwestern San Luis Potosí. The specimens from both localities are in the USNM.

Specimens examined. A total of 65 specimens from:

ZACATECAS. Cañitas, 3 (USNM); Villa de Cos, 6,700 ft, 2 (KU); 4.5 mi E Fresnillo, 1 (MVZ); 8 mi SE Zacatecas, 7,225 ft, 3 (KU); 5 mi S Ojo Caliente, 2 (UI); Berriozabal, 4 (USNM); Real Di Pinos [=Pinos], 4 (AMNH).

AGUASCALIENTES. 7 mi N Rincón, 1 (UI); 4.5 mi N Rincón de Romos, 5 (UI); 1 mi S, 6 mi E Rincón de Romos, 6,550 ft, 2 (KU); 1 mi N Chicalote, 1,900 m, 1 (MVZ); Chicalote, 11 (USNM).

SAN LUIS POTOSÍ. 4.5 mi SW Herradura, 7,200 ft, 3 (KU); 8 mi W Ramos, 6,700 ft, 1 (KU); Hacienda La Parada, 5 (USNM); Jesús María, 17 (USNM).

Additional records. SAN LUIS POTOSÍ. 2 km E Illescas, 13 (LSU, Dalquest, 1953:118); 8 mi SW Ramos, 6,700 ft, 1 (KU); 7 km NW Palmas, 1 (LSU, Dalquest, 1953); Salinas, 1 (LSU, Dalquest, 1953); 4 km E Salinas, 1 (LSU, Dalquest, 1953).

Dipodomys spectabilis nelsoni Merriam

Dipodomys nelsoni Merriam, Proc. Biol. Soc. Washington, 20:75, 22 July 1907, original description.

Type. Male, young adult, skin and skull; No. 79439, U. S. Biological Surveys Collection; from La Ventura, Coahuila, México; obtained by E. W. Nelson and E. A. Goldman, 10 August 1896, original number 9998.

Range. Southeastern Chihuahua, northeastern Durango, western and southern Coahuila, northern Zacatecas, northern San Luis Potosí, and southern Nuevo Leon.

More specifically, in southeastern Chihuahua from the vicinity of Escobillas, west to the eastern valley of the Río Conchos, south to the vicinity of Ciudad Camargo, Búfalo, and Salaíces; to the vicinity of La Zarca in northeastern Durango, and southeast to the vicinity of Casco and to a place 10 miles southwest of Yerbanís in east central Durango; in northwestern Coahuila from the southern valley of the Río Grande in the vicinity of Boquillas, south to the vicinity of Tanque Alvarez, and Ocampo, and southeast to the eastern border of the state; in northeastern Zacatecas to the vicinity of San Tiburcio; southeast to the vicinity of Matehuala in northeastern San Luis Potosí; and to Doctor Arroyo in southern Nuevo Leon. Except in the northwestern part, limits of the range are not well known, and more collecting along the periphery of the range is needed to establish its extent and limits.

Diagnosis.

Size: Small; adult total length 302.0 to 325.0 mm; tail length 176.0 to 196.0 mm; body length 118.0 to 134.0 mm; hind foot length 42.0 to 49.0 mm; ear length 14.0 to 16.5 mm; distal white of tail short, 6.0 to 19.9 mm.

Color: In general, Light Ochraceous-Buff to grizzled buff, purest on sides, thinly mixed with black-tipped hairs on dorsum, especially over top of head, back and rump; arietiform markings dusky; anterior ear fold dusky; large spot behind ankle blackish; plantar stripes light brown to dark brown; tuft of hairs at base of tail ventrally grayish black; dorsal and ventral tail stripes dusky; subterminal band of tail dusky to black and sometimes tufted.

Skull: Small-sized; greatest length 41.5 to 43.2 mm; basal length 29.7 to 32.0 mm; nasals short, 14.8 to 15.4 mm; maxillary arch rela-

tively heavy and not flared; breadth across maxillary arches 22.2 to 24.4 mm; auditory bullae relatively large; greatest breadth across bullae 26.3 to 27.6 mm; supraoccipital and interparietal usually small; external opening of auditory meatus usually oval; incisors narrow; mandibular length small, 17.1 to 18.5 mm. Also see Table 6.

Comparisons. For comparisons with *Dipodomys spectabilis spectabilis, D. s. zygomaticus,* and *D. s. cratodon,* see accounts of those subspecies (pp. 31, 49, 53).

Remarks. Typical *Dipodomys spectabilis nelsoni* is characterized by Light Ochraceous-Buff to grizzled buff color on the dorsum, small external size, and a short white tip of the tail. The skull is small, the maxillary arches are not flared, and the auditory bullae are small.

Merriam (1907:75) described the species "*D. nelsoni*" as "Similar to *spectabilis* in general form and massiveness of skull but much smaller . . . mastoids actually nearly as large—relatively larger—than *spectabilis*; . . . white tip of tail shorter (20 mm) or absent all together." Generally, the white tip of the tail is short (the shortest measured is 3 mm), but it is never absent (unless it is broken). When this white end of the tail is short, it is usually covered with the long blackish fur of the subterminal dark band of the tail and thus not readily seen.

Since Merriam's description of *nelsoni,* several investigators—Dalquest (1953:119); Baker (1956:246); and Anderson (1972:313), to name three—have studied the relationship between "*D. nelsoni*" and *D. spectabilis* and have arrived at similar conclusions. They maintain that the two forms are closely related, but there is no evidence of intergradation between them and they do not overlap in their ranges. Thus *nelsoni* has retained its specific status. However, Baker and Greer (1962:101), commenting on *nelsoni* in Durango, stated that "there is indication that some contact between the two species has occurred in extreme north central Durango, possibly resulting in hybridization."

The geographic range of *D. s. nelsoni* complements the ranges of the other subspecies of *D. spectabilis* (Figs. 2 and 6). No conclusive evidence is yet available to indicate that specimens with the characters of these two taxa were collected from the same place. Four of five specimens in the U. S. National Museum labeled as Santa Rosalia [=Ciudad Camargo] are *D. s. zygomaticus* and the fifth one is *D. s. nelsoni.* Three of the four *zygomaticus* and the specimen of *nelsoni* were collected by E. W. Nelson between 17 and 26 September 1893. In

his field notes, Nelson wrote about his field number 5482 (the *nelsoni* specimen) as being found only on the mesa land back from the river. It is not known on what side of the river this specimen was collected, and whether the specimens of *zygomaticus* were collected at the same place or not. Goldman (1951:124) reported that all the work in Santa Rosalia during the aforementioned period was done within a radius of three miles, mainly along the sides of the river bottom and adjacent mesa above town.

The subspecies of *D. spectabilis* closest to the range of *nelsoni* is *zygomaticus*. Material recently collected from critical localities by the Museum of Natural History, University of Kansas, from south central Chihuahua, brings the range of *D. s. zygomaticus* to approximately 2 miles from that of *D. s. nelsoni* (*zygomaticus* from 19.5 mi WSW Jiménez; *nelsoni* from 1 mi S Salaíces, Chihuahua). This and other material obtained by The Museum, Michigan State University, from north central Durango, show strong evidence of intergradation.

The zone of intergradation between *D. s. zygomaticus* and *D. s. nelsoni* is a secondary one. This is evident by its narrowness and by the steep slope of the character gradient. In general, specimens of *D. s. zygomaticus* become smaller in all measurements as they approach the zone of contact, and along this zone they are extremely variable. Within one sample there are specimens typical of *zygomaticus* and others which are distinctly smaller, and, in this respect, closer to *nelsoni*. Specimens of *D. s. zygomaticus* in this area show a pronounced tendency to resemble *D. s. nelsoni* in color, in having a shorter white tip of the tail, and in having smaller external and cranial measurements than typical *zygomaticus*. This is more prominent among specimens from the localities closest to the range of *nelsoni* (1 mi S Búfalo; 19.5 mi WSW Jiménez, Chihuahua) and also among specimens from 12 mi WSW La Resolana, Durango. Most specimens of *D. s. zygomaticus* from the zone of contact have parallel jugals and are thus not typical of this subspecies.

Specimens of *D. s. nelsoni*, in this zone of contact, seem to be more conservative in the shift of the characters, and the change is less than in *D. s. zygomaticus*. Nevertheless, these specimens and others from nearby localities show a tendency to resemble *D. s. zygomaticus* in color, and in being larger in external and in cranial measurements, at least in some specimens. This is well illustrated in specimens from 1 mi S Salaíces (the closest locality to the range of *zygomaticus*).

Of the 20 measurements taken, 19 of them in the zone of intergradation show overlap of varying degrees (Fig. 9). The only measurement that does not show any overlap is the breadth across the maxillary

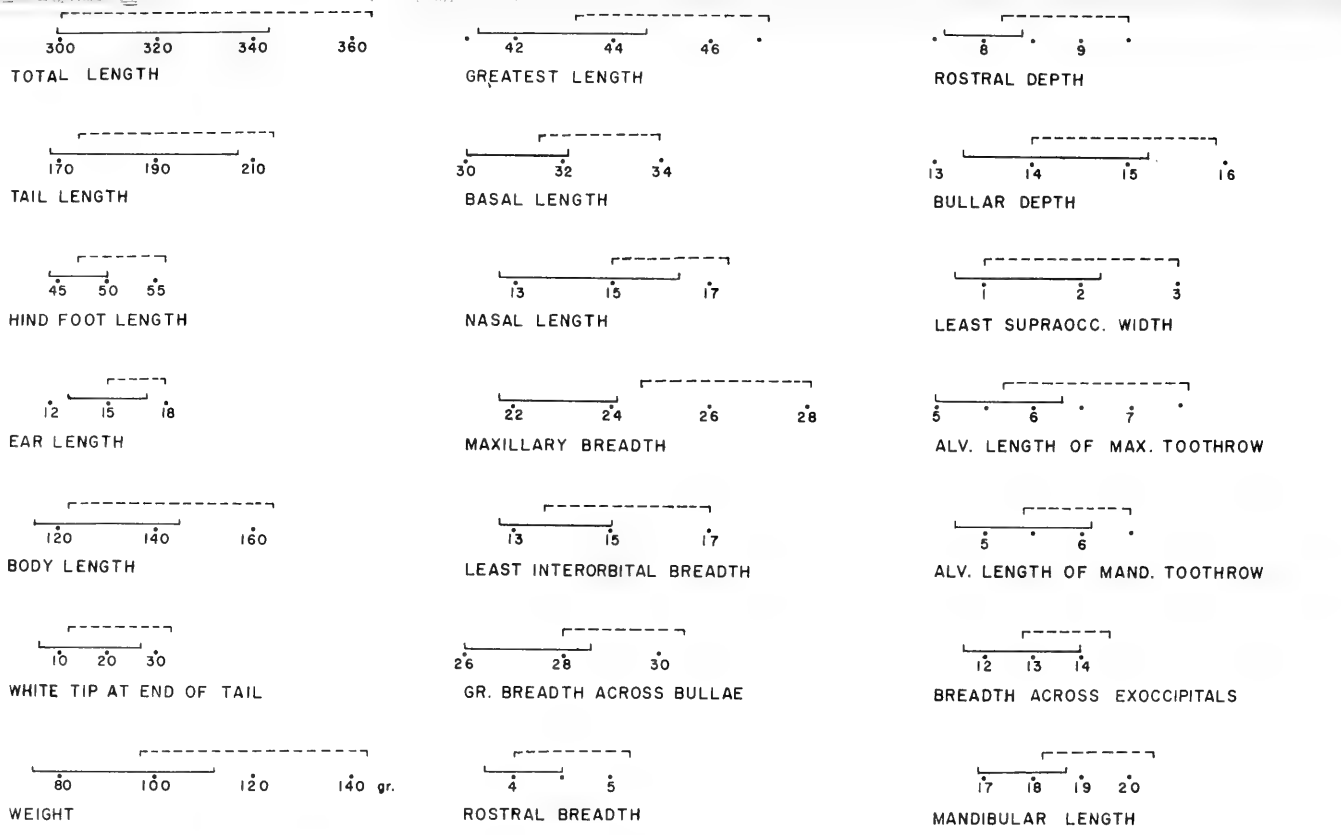


Fig. 9. Linear overlap between the external measurements, weights, and fourteen cranial measurements of adult specimens of *D. s. zygomaticus* (broken lines) and *D. s. nelsoni* (solid lines) from the zone of intergradation in south central Chihuahua and north central Durango.

arches. There is, however, a clear indication that this character in *D. s. zygomaticus* does become smaller in the zone of intergradation. In my opinion, this difference is not important, for there is only a 0.5-mm break between the two measurements. The bullar index for all the adults from this zone is 1.184 for *nelsoni* and 1.107 for *zygomaticus*. This difference between the two indices is small. Intensive collecting in this zone of intergradation almost certainly will yield specimens exhibiting overlap in maxillary breadth, and a still greater degree of overlap in the other characters.

In his discussion of the relationship between *D. spectabilis* and *D. nelsoni*, Stock (1974:523) indicated that both species have a karyotype with a diploid count of 72. He also stated that the subspecies of *D. spectabilis* differ from each other in the same way that they differ from *D. nelsoni*, but to a lesser degree. These conclusions strongly support my argument in regarding *D. nelsoni* as a subspecies of *D. spectabilis*. Unfortunately, Stock did not have samples of the southern subspecies of *D. spectabilis*. If he had had karyotypes of specimens of *D. s. zygomaticus* to compare with *D. nelsoni*, he might have noted an even closer relationship between these two.

Specimens from the western part of the range of *D. s. nelsoni* in eastern Durango are larger than typical *nelsoni*. Although *D. s. nelsoni* is presently not known to be in contact with *D. s. cratodon*, specimens from northern San Luis Potosí and southern Nuevo Leon are larger than typical *nelsoni*. Also, as noted in *Remarks* under *D. s. cratodon*, specimens of this subspecies from southeastern Zacatecas and northwestern San Luis Potosí are slightly smaller in many characters than the typical. This small size in specimens of *cratodon* in this part of its range, and the large size in specimens of *nelsoni* in northern San Luis Potosí and southern Nuevo Leon may suggest intergradation between these two forms.

D. s. nelsoni is found in a variety of habitats and at a wide range of elevations. The animal seems to be best adapted to open desert habitat from elevations as low as 1,800 feet in the vicinity of Boquilla in northwestern Coahuila, up to 3,300± feet in the vicinity of Ocampo in central Coahuila. It also is found in mixed grassland and thorn shrubs along the periphery of the range, at least in eastern Durango in the vicinity of La Zarca at 6,650 feet elevation. Nevertheless, *D. s. nelsoni* and *D. s. zygomaticus* inhabit similar areas along the periphery of their ranges in south central Chihuahua and north central Durango. Also, *nelsoni* is found in a transitional area between desert and grassland in east central Durango (Baker and Greer, 1962:100). This habitat is similar to that in which *D. s. spectabilis* occurs.

On the basis of the above mentioned data, *nelsoni* is regarded as a subspecies of *D. spectabilis*. The zone of secondary intergradation shows the highest degree of concordance in the characters examined, and *D. s. nelsoni* is the most distinct subspecies of *D. spectabilis*.

It is probable that *D. s. nelsoni* became isolated sometime before the isolation of *D. s. cratodon*. This latter race inhabits habitat similar to that of subspecies found in Arizona, New Mexico, western Texas, and Chihuahua and probably very little change has occurred in the habitat since *cratodon* was isolated. *D. s. nelsoni* is found in a somewhat different habitat, and because of the length of the period of isolation and differences in the habitat, the morphological differentiation of this subspecies is greater than that of *D. s. cratodon*. The long isolation of *nelsoni* has brought enough morphological differentiation to achieve nearly specific status. The contact between *D. s. nelsoni* and *D. s. zygomaticus* seems to be relatively recent in the evolutionary and distributional histories of the species.

The range of *D. s. nelsoni* occurs in only the eastern part of Durango as far as the eastern slopes of the Sierra Madre Occidental and does not extend westward beyond the eastern valley of the Río Oro in the north central part of that state. The Río Grande seems to be an effective barrier for *D. s. nelsoni* inasmuch as it is not present in the northern valley of the river in south central Texas. Although the habitats on the two sides of the river in this region are similar, it is unlikely that future collecting on the northern side of the river will yield specimens of *D. s. nelsoni*. The range of this subspecies most probably will not extend much farther to the northeast of Coahuila because of the presence of the Sierra del Carmen and the Sierra Madre Oriental. Future collecting may reveal a wider distribution in northern Zacatecas and northern San Luis Potosí.

Five specimens of *D. s. nelsoni* from two localities in Zacatecas represent the first records for that state.

Specimens examined. A total of 227 specimens from:

CHIHUAHUA. 8 mi NNW Escobillas, 5,000 ft, 4 (KU); 1 mi E Julimes, 8 (KU); 3 mi E Julimes, 3,850 ft, 1 (KU); 4 mi E Julimes, 3,850 ft, 1 (KU); 1 mi W San Francisco, 4,325 ft, 1 (KU); 2 mi N, 6 mi E Camargo, 4,150 ft, 3 (KU); 1 mi N, 3 mi E Camargo, 4,150 ft, 2 (KU); Santa Rosalia [=Ciudad Camargo], 1 (USNM); Sierra Almagre, 12 mi S Jaco, 5,300-6,000 ft, 10 (KU); Sierra Almagre, SW slope, 19 mi S, 4 mi E Jaco, 5,500 ft, 11 (KU); 23 mi ESE Boquilla, 4,700 ft [about 4 mi E Búfalo], 4 (KU); 23.5 mi ESE Boquilla, 4,700 ft, 2 (KU); 9 mi N Jiménez, 2 (KU); 2 mi W Jiménez, 4,700 ft, 1 (KU); 5 km S Jiménez,

TABLE 6

Measurements (in mm) of adult specimens from type-localities or near type-localities of the different subspecies of *Dipodomys spectabilis*.

(Mean with sample size as superscript and range below)

Character	*spectabilis* 3♂♂, 1♀	*perblandus* 2♂♂, 4♀♀	*intermedius* 4♂♂, 3♀♀
Total length	347.8[4]	326.6[5]	325.0[6]
	340.0 — 353.0	315.0 — 335.0	314.0 — 330.0
Tail length	203.3[4]	193.6[5]	186.7[6]
	199.0 — 206.0	184.0 — 204.0	180.0 — 195.0
Hind foot length	52.3[4]	48.3[6]	47.4[7]
	51.0 — 53.0	47.0 — 50.0	46.0 — 49.0
Ear length	16.8[4]	—	16.6[7]
	16.0 — 17.0		16.0 — 17.0
Body length	144.5[4]	133.2[6]	137.4[7]
	141.0 — 149.0	130.0 — 138.0	130.0 — 146.0
Greatest skull length	45.9[4]	44.4[6]	43.0[5]
	44.0 — 46.8	43.0 — 45.3	42.1 — 44.2
Basal skull length	33.3[4]	31.8[5]	31.0[4]
	32.0 — 34.2	31.6 — 32.1	30.5 — 31.8
Length of nasals	17.1[4]	16.1[6]	15.8[7]
	16.7 — 17.5	15.0 — 16.8	15.2 — 16.8
Breadth across maxillary arches	26.3[4]	25.7[4]	25.0[7]
	25.8 — 26.6	25.3 — 25.9	24.2 — 25.9
Least interorbital breadth	15.9[4]	14.6[4]	14.8[7]
	15.7 — 16.3	14.0 — 15.3	14.1 — 15.3
Greatest breadth across bullae	29.4[4]	28.1[6]	27.3[4]
	28.3 — 30.2	27.7 — 28.6	27.2 — 28.7
Rostral breadth	4.6[4]	4.6[6]	4.3[7]
	4.4 — 4.8	4.3 — 4.7	4.1 — 4.4
Rostral depth	8.8[4]	8.5[6]	8.4[7]
	8.5 — 9.0	8.3 — 8.7	8.2 — 8.6
Bullar depth	15.4[4]	14.8[6]	14.6[6]
	14.9 — 15.9	14.5 — 15.1	14.2 — 15.2
Alveolar length maxillary toothrow	6.5[4]	5.9[6]	5.9[7]
	6.1 — 6.8	5.6 — 6.2	5.3 — 6.3
Least breadth supraoccipital	1.7[4]	2.1[6]	1.9[5]
	1.5 — 2.0	1.9 — 2.5	1.4 — 2.2
Breadth across exoccipitals	15.1[3]	13.6[6]	13.1[4]
	14.7 — 15.7	12.8 — 14.2	12.7 — 13.4
Alveolar length mandibular toothrow	6.1[4]	5.8[6]	5.6[7]
	5.8 — 6.3	5.5 — 6.2	5.3 — 6.1
Mandibular length	19.7[4]	18.7[6]	18.0[7]
	18.6 — 20.2	18.5 — 19.1	17.3 — 18.5
Length white tip of tail	40.8[4]	23.0[5]	20.0[7]
	37.0 — 46.0	16.0 — 30.0	13.0 — 25.0
Weight, grams	—	—	98.7[7]
			94.8 — 105.7

spectabilis: 19 mi W, 2 mi N Willcox, Cochise County, Arizona
perblandus: Calabasas, Santa Cruz County, Arizona
intermedius: 16.7 mi SW Bámori, Sonora

baileyi 6♂♂, 7♀♀	*zygomaticus* 3♂♂, 1♀	*cratodon* 5♂♂, 4♀♀	*nelsoni* 11♂♂, 3♀♀
354.6[11]	341.5[4]	337.0[8]	319.2[13]
340.0 — 373.0	334.0 — 352.0	320.0 — 358.0	303.0 — 334.0
205.4[11]	201.6[4]	209.0[8]	197.7[13]
191.0 — 221.0	195.0 — 212.0	195.0 — 226.0	180.0 — 211.0
55.0[12]	52.3[4]	52.5[8]	48.5[14]
53.0 — 56.0	49.0 — 54.0	51.0 — 54.0	46.0 — 51.5
13.1[12]	—	—	—
12.0 — 14.0			
150.1[12]	139.9[4]	128.2[8]	121.1[14]
142.0 — 164.0	138.0 — 143.0	117.0 — 133.0	108.0 — 132.0
47.0[12]	45.7[4]	45.4[9]	42.3[14]
45.5 — 48.7	45.0 — 46.2	43.4 — 47.0	40.6 — 43.5
34.6[10]	34.1[4]	34.1[9]	31.1[14]
33.8 — 35.7	33.7 — 34.3	32.5 — 35.5	29.6 — 32.0
17.0[13]	16.1[4]	16.2[9]	14.9[14]
16.1 — 17.7	15.8 — 16.5	15.2 — 17.1	14.2 — 15.5
26.9[12]	26.9[3]	26.9[8]	23.0[13]
25.6 — 28.3	26.0 — 27.6	25.9 — 28.5	22.2 — 23.7
15.3[13]	16.1[2]	16.0[7]	14.5[11]
14.8 — 16.3	15.7 — 16.4	15.3 — 17.0	14.0 — 15.3
29.7[10]	30.3[4]	29.3[9]	26.8[14]
28.8 — 31.4	29.7 — 30.9	28.4 — 30.5	25.7 — 27.9
5.0[13]	5.0[4]	4.6[9]	4.2[13]
4.5 — 5.5	4.8 — 5.3	4.4 — 5.0	3.7 — 4.7
9.2[13]	9.1[4]	9.1[9]	7.9[14]
8.9 — 9.6	8.9 — 9.4	8.7 — 9.4	7.6 — 8.2
15.7[10]	15.3[4]	15.5[9]	14.5[14]
15.1 — 16.9	14.9 — 15.6	15.2 — 16.0	13.8 — 15.1
6.6[13]	6.6[4]	6.7[9]	6.0[14]
6.0 — 7.0	6.4 — 6.7	6.4 — 6.9	5.3 — 6.8
2.2[13]	2.0[4]	1.4[9]	1.4[14]
1.3 — 2.6	1.7 — 2.2	0.9 — 1.7	1.0 — 1.8
14.4[10]	14.3[3]	14.4[9]	13.0[12]
13.5 — 15.2	13.8 — 15.0	13.4 — 16.0	12.2 — 14.1
6.2[13]	6.0[4]	6.3[9]	5.7[14]
5.7 — 6.7	5.3 — 6.5	6.1 — 6.5	5.4 — 6.0
20.4[13]	19.8[4]	20.6[9]	17.7[14]
19.3 — 21.4	19.3 — 20.4	19.8 — 21.9	17.1 — 18.4
30.0[13]	22.8[4]	19.8[8]	11.6[11]
24.0 — 40.0	18.0 — 29.0	12.0 — 24.0	4.0 — 20.0
146.2[13]	—	—	—
128.9 — 164.3			

baileyi: 44 mi NW Roswell, Lincoln County, New Mexico
zygomaticus: Parral, Chihuahua
cratodon: Chicalote, Aguascalientes
nelsoni: La Ventura, Coahuila

4 (KU); 10 mi WSW Jiménez, 4,800 ft, 2 (KU); 11.5 mi WSW Jiménez, 4,800 ft, 2 (KU); 12.5 mi SW Jiménez, 5,000 ft, 3 (KU); 14.5 mi WSW Jiménez, 5,000 ft, 4 (KU); 1 mi S Salaíces, 4,900 ft, 21 (KU); 6.9 mi NE Escalón, 1 (UI); Escalón, 60 km SE Jiménez, 2 (KU), 10 (USNM).

DURANGO. 6 mi E Zavalza, 4,150 ft, 3 (MSU); 7 mi NW Yermo, 3,900 ft, 1 (MSU); 7 mi NNW La Zarca, 6,000 ft, 1 (MSU); 12 mi E La Zarca, 6,000 ft, 4 (KU); 14 mi E Zarca, 6,650 ft, 1 (MVZ); 35 mi W Mapimi, 5,500 ft, 3 (MSU); 1 mi WSW Mapimi, 3,800 ft, 3 (KU); 4 mi SE Casco, 5,850 ft, 1 (MSU); 2 mi NW Chocolate, 4,500 ft, 3 (KU); 2 mi E Pedriceña, 4,300 ft, 6 (KU), 1 (MSU).

COAHUILA. 7 mi S, 2 mi E Boquillas, 1,800 ft, 2 (KU); 6 mi N, 2 mi W Castillón, 3,750 ft, 1 (KU); 2 mi SSE Castillón, 4,050 ft, 2 (KU); 11 mi N, 9 mi W Tanque Alvarez, 4,500 ft, 1 (KU); 2.5 mi SE Ocampo, 3,300± ft, 1 (KU); 2.5 mi W, 21 mi S Ocampo, 3,500± ft, 4 (KU); 4 mi N Acatita, 3,600 ft, 2 (KU); Treviño, 2 (USNM); 15 mi SSE Hda. Guadalupe [=Guadalupe], 3,200 ft, 1 (MSU); Jaral, 11 (FMNH), 1 (UCLA), 3 (USNM); ½ mi S San Antonio de Jaral [=Jaral], 4,400 ft, 6 (MVZ); 12 mi N, 10 mi E Parras [=Parras del Fuente], 5,000 ft, 1 (KU); La Pastora, 4 mi W, 15 mi N Saltillo, 1 (KU); 3 mi N, 5 mi W La Rosa, 3,600 ft, 3 (KU); Torreon, 1 (USNM); 1 mi N San Lorenzo, 4,200 ft, 4 (KU); 4 mi NNW Saltillo, 5,200 ft, 4 (KU); N foot Sierra Guadalupe, 10 mi S, 5 mi W General Cepeda, 6,500 ft, 16 (KU); W foot, Pico de Jimulco, 4,600 ft, 1 (KU); 7 mi S, 1 mi E Gómez Farías, 6,500 ft, 5 (KU); San Juan Neponuceno, 5 mi La Ventura, 1 (MVZ); La Ventura, 18 (USNM).

ZACATECAS. 3 mi N Lulú, 4 (MVZ); 1 mi SWS S[an] Tiburcio, 7,000 ft, 1 (KU).

SAN LUIS POTOSÍ. 57 mi N Matehuala, 6,000 ft, 1 (AMNH); 11 mi NW Cedral, 1 (MVZ).

NUEVO LEÓN. Doctor Arroyo, 2 (USNM).

Additional records. CHIHUAHUA. (All from Anderson, 1972:313) "Piñon Camp" Sierra Rica, 4,900 ft, 1 (SRSC); "Alluvial flat between camps", 3,200 ft (E Sierra Rica), 2 (SRSC); "29° 12′ N, 104° 06′ W", 3,200 ft, 1 (SRSC).

DURANGO. 10 mi SW Yerbanís, 6,200 ft (Baker and Greer, 1962: 100).

COAHUILA. Near Cuatro Ciénegas (Gilmore, 1947:158); about 32 mi N Saltillo (Baker, 1956:244).

SAN LUIS POTOSÍ. 3 km S Matehuala, 1 (LSU, Dalquest, 1953:19); 6 km S Matehuala, 1 (LSU, Dalquest, 1953:19).

DIPODOMYS DESERTI

Species Characteristics

The desert kangaroo rat is the most specialized and one of the largest species of the genus *Dipodomys*. It is adapted to live in the lowest, hottest, and most arid regions of North American deserts. It has four toes on each hind foot, and the foot is covered with relatively long hairs. The color of the upper parts varies from Pale Buff to Ochraceous Buff mixed with a variable amount of long blackish hairs, depending on the subspecies. The supraorbital and postauricular spots, hip stripes, fore limbs, dorsal surface and sides of hind feet, the ring at the base of the tail, including the ventral tuft, lateral tail stripes, ventral surface of the body, and the distal tip of the tail are pure white. The skull is large, with maximum inflation of the bullae for the genus (Fig. 10). The supraoccipital is so restricted dorsally as to be almost absent, and the interparietal is usually absent in adult specimens. The nasals are long and the rostrum is long and slender. The maxillary arches are not heavy or wide, and give the skull a triangular appearance. The jugals are divergent posteriorly. The molariform teeth are of the kleistodont type (Nader, 1966). External openings of the auditory meati are large and oval-shaped. The ectoglenoid fossa is absent. The mandibles are delicately built. The weight of adult males ranges from 91.0 to 148.0 grams, of adult females, from 82.8 to 141.2 grams.

The hyoid apparatus of *Dipodomys deserti* consists of only two parts, as in *D. spectabilis*, a basihyal and a reduced thyrohyal. The basihyal is large with a low ventral ridge. The anteromedial border of the "shoulders" is more or less pointed. The basihyal arch is usually deep. The thyrohyal is large. Secondary sexual dimorphism is evident in this structure.

This large kangaroo rat primarily inhabits the Lower Sonoran Life-zone, but it also invades the salt-desert area (Hall, 1946:34) of the

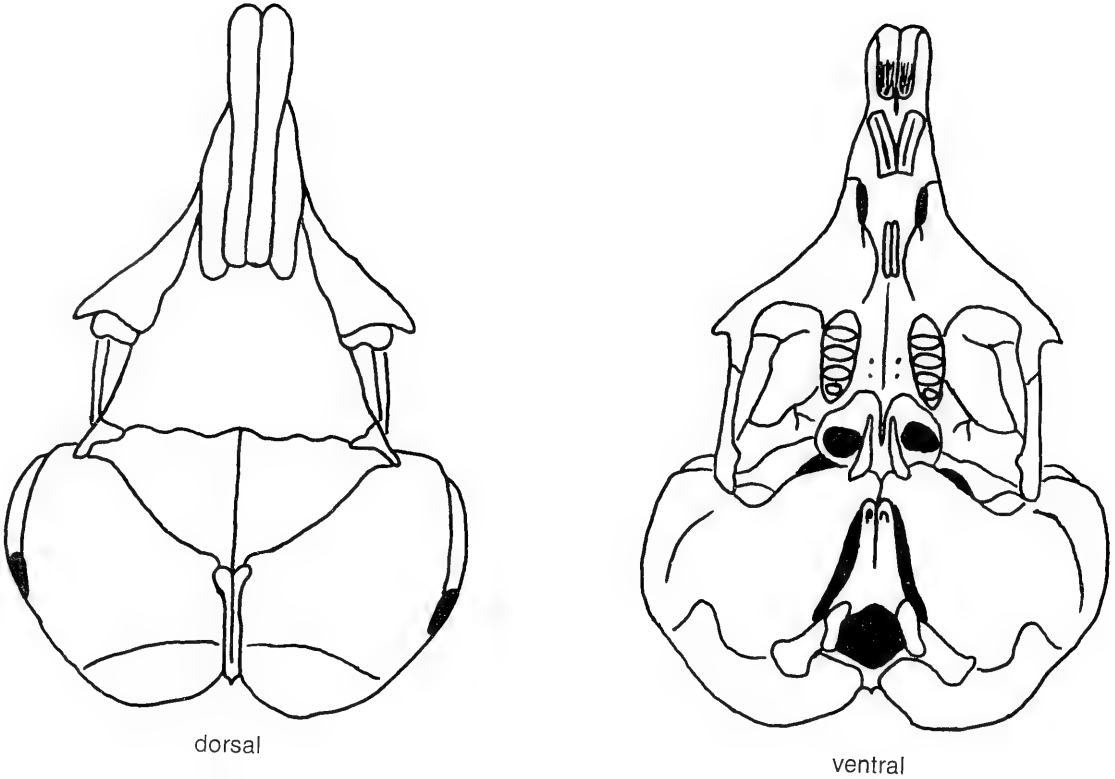


Fig. 10. Dorsal and ventral views of *Dipodomys deserti deserti* skull, UI No. 17578 ♂ from 6 mi SE Somerton, Yuma County, Arizona.

Fig. 11. Beaver Dam Wash, at Terry's Ranch, 7 mi N Utah-Arizona border, Washington County, Utah. Typical habitat of *Dipodomys deserti deserti.*

Upper Sonoran Life-zone in northwestern Nevada. It is restricted almost exclusively to the loose sandy parts of the desert with scattered creosote bush, *Larrea* sp. and mesquite, *Prosopis* sp. (Fig. 11). In only one case was *D. deserti* found in gravelly soil and that was in the vicinity of Florence in central Arizona (see *Remarks* under *D. d. arizonae*, p. 94). This species is well adapted to a wide range of elevations within its geographic limits. It inhabits the desert depressions as low as −200 feet at Salt Creek, Inyo County, in the Death Valley National Monument, California. It was collected at elevations as high as 5,700 feet in the Huntoon Valley, Mineral County, Nevada.

Other kangaroo rats that occur sympatrically with *Dipodomys deserti* are *D. merriami, D. ordii, D. panamintinus,* and *D. microps.* Its size, coloration, and skull features make *D. deserti* readily distinguishable from all of these other kangaroo rats.

Little is known about the longevity of this rodent. The only available record is that of Brattstrom (1960:404) who reported a captive *D. d. deserti* living for five years and five months. An adult *D. d. arizonae* was live-trapped on 3 February 1961 and kept in captivity at the Museum of Natural History, University of Illinois, until it died on 26 September 1969, having lived in captivity for 7 years and about 8

months. Since this animal was adult when captured, it lived at least 8½ to 9 years. This is the longest record of longevity for the desert kangaroo rat and, to my knowledge, it is the longest record for the genus. Lidicker (1960:136) reported a Merriam's kangaroo rat living at least 7½ to 8 years.

Records of predators of *D. deserti* are scarce, and this species seems to be successful in avoiding its natural enemies. The kit fox, *Vulpes macrotis*, owls, and snakes may be among its predators. Grinnell *et al.* (1937:417) concluded that kangaroo rats constitute the main food of the kit fox in the soft sand areas of California where *D. deserti* lives. McAtee (1921:258) reported that in 592 pellets of the barn owl, *Tyto alba*, collected in California, remains of 230 kangaroo rats were found in addition to other rodents, but no mention was made of the kinds of kangaroo rats involved.

Records of ectoparasites and endoparasites are seemingly very few. *D. deserti* is known to be host for two species of fleas, *Meringis parkeri*, and *Thrassis* (*Thrassoides*) *hoffmani* (Hubbard, 1961:135) and one species of sucking louse, *Fahrenholzia pinnata* (Ferris, 1922:160). No record of endoparasites was found.

As with *D. spectabilis*, all specimens examined were checked for molting and notes on molting patterns were taken. The number of molting specimens was noticeably small. Although at least one specimen was molting in each month, with the exception of November and December (Table 7), there seems to be only one adult molt per year, occurring in the spring and the summer, with a peak in July. These data show that the time of molt is in disagreement with the findings of Grinnell (1922:107) who stated that molt in *D. deserti* takes place in the fall.

REPRODUCTION

Knowledge of the reproductive activity in the desert kangaroo rat is

TABLE 7
Number of molting individuals of *Dipodomys deserti*
(by age-groups and month of capture)

	Month of capture											
Age-Group	J	F	M	A	M	J	J	A	S	O	N	D
Juvenile	—	—	—	—	4	6	—	—	—	—	—	—
Immature	—	1	—	3	4	4	4	2	1	—	—	—
Subadult	—	1	—	3	4	3	1	2	—	—	—	—
Adult	3	—	1	—	4	7	17	4	1	1	—	—

TABLE 8
Distribution of recorded reproductive activity in females of *Dipodomys deserti* by age-groups

	Immature	Subadult	Adult	Total
Number of females examined	5	23	77	105
Females showing reproductive activity	2	10	48	60

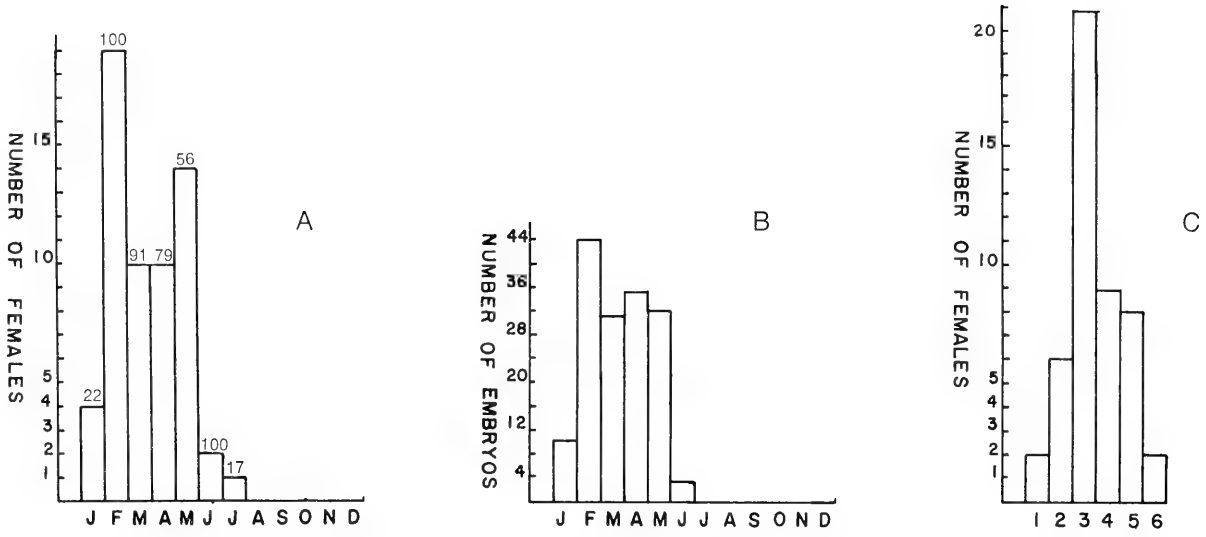
meager. Of 105 females examined for pregnancy or lactation, 60 (57.1%) showed signs of such activities (Table 8). Sexual maturity begins early in the life of this species. In five immature females, one was lactating and another had four embryos; among 23 subadults, 10 were pregnant.

Reproductive activity starts early in January and continues through the first half of July. The first recorded pregnancy is on 18 January (3 embryos × 30 mm) and the latest reproductive activity is a lactating female on 10 July, with pregnancies in every month between (Fig. 12A). No differences in the time of pregnancy between the northern and the southern populations were detectable. The month of February has the largest number of pregnant females and the largest number of young born, judged from the number of embryos (Fig. 12 A and B). All the females examined in this month were pregnant.

The breeding period is relatively long, spreading over seven months, from January to July. Two peaks are recognized within the breeding period, in February and in May (Fig. 12A). This leads to the assumption that two litters are produced in the year, but no final conclusion can be made until further study is done in this respect.

The number of embryos per litter ranges from one to six (Fig. 12C). In 48 pregnant females the number of embryos was 165, with a mean of 3.43 embryos per female and a mode of 3. Butterworth (1961b:414) reported similar figures from a captive pair. The female produced 23 young in seven litters with a mean of 3.29 young per litter and a mode of 3. Butterworth also reported that the gestation period varies between 29 and 32 days. The lengthening of the gestation period in *D. deserti* (one of the longest in the genus) reflects a unique adaptation to produce well-developed young that survive the severe conditions of the desert habitat. A newborn is about 52 mm in total length (Butterworth, 1961a:134).

Little is known about growth and development of the desert kangaroo rat. Butterworth (1961a) reports that the incisors erupt between 7 and 10 days after birth, weaning occurs between 15 and 25 days,



A. Number and percentage (above each column) of females showing reproductive activity per month

B. Number of embryos per month

C. Frequency distribution of litter size

Fig. 12. Reproductive activity in *Dipodomys deserti*.

adult size is attained at about 90 days and very little growth takes place after that; 91% of weight is attained in 90 days, and an average adult weight in 150 to 180 days.

COLOR

In *Dipodomys deserti* the color of the upper parts varies from pale fawn to grayish black, depending on the subspecies. In the zone of intergradation between the different subspecies, there are all degrees of color gradients. Within a given subspecies, color is usually stable except in *D. d. deserti* where it varies from Pale Buff to Ochraceous Buff thinly mixed with long dusky colored hairs (see *Remarks* under this subspecies, p. 86). Color, in general, is a useful taxonomic criterion; however, color variations may be present within one subspecies —as in *D. d. deserti*—and in this case cranial characters are relied on almost exclusively for diagnosis.

The subspecies of *D. deserti* do not exhibit any noticeable variation in the white supraorbital and postauricular spots, hip stripe, venter, forefeet, dorsal surface and sides of the hind feet, ring at the base of the tail, and the lateral tail stripes. Occasionally the supraorbital and postauricular spots are not too distinct in *D. d. deserti* from California and are more distinct and usually larger in *D. d. arizonae*. Although the distal white of the tail is quite variable within most of the samples, it is usually short in *D. d. deserti*, longer in *D. d. arizonae*, and longest in *D. d. sonoriensis*. There are noticeable differences in the extent of the color of the arietiform markings between the subspecies. In *D. d. deserti*, this marking ranges from nearly obliterated to a pale buffy line, while in *D. d. arizonae*, *D. d. sonoriensis*, and *D. d. aquilus* it is dusky to blackish. The color of the orbital ring follows almost the same pattern as that of the arietiform markings. The outer surface of the ear is similar in color to the upper parts.

The plantar stripe also shows some variation in color. In *D. d. deserti* it ranges from absent to light brownish which is usually restricted to the heel region, while in the other subspecies it is most frequently brownish or blackish. A yellow or yellowish shade is sometimes present on the ventral side of the toes. The dorsal tail stripe and the subterminal dark band of the tail vary, in general, according to the color of the pelage. It is buffy or dusky in *D. d. deserti* and blackish mixed with gray in the other subspecies. The ventral tail stripe is ordinarily absent in *D. d. deserti* but, when present, it is pale-colored and broken. It is usually present in *D. d. sonoriensis* and *D. d. aquilus*, and always present in *D. d. arizonae*, where it is dark and most often continuous.

The color of the pelage of *D. deserti* seems to be correlated with the color of the soil. Pale-colored populations are found in the central part of the range in the Mojave, Colorado, and Yuma deserts, where the soils of the desert are mostly pale or buff in color (Dice, 1939:120). The color of the specimens in the northwestern populations (in NW Nevada) is dark and so is the color of the soil. The palest-colored individuals are found in Death Valley, California, where the hottest and the driest conditions occur within the range of the species. High alkalinity of the soil affects the color in *D. d. deserti*, and the upper parts become more yellowish than usual; the plantar stripes, the distal white of the tail, and in extreme cases, the circumanal ring are altered in color. The original color is restored after molting. Such altered coloration was found among specimens from Keeler and from several localities within Death Valley National Monument, California, and in some specimens from southern Nevada, especially Thorpes Mill in Nye County. The ochraceous color of the populations in southwestern Arizona and northwestern Sonora is not likely to have been caused by the alkalinity of the soil, as most of these specimens have fresh pelages. Several specimens of *D. d. deserti*, especially in California and southern Nevada, have one or more buffy spots on the ventral side. Similar spots were not seen in the other subspecies. It is not known whether these spots are genetically controlled or adventitious.

Age Variation

Four age-groups were distinguishable for *Dipodomys deserti*. These are established on the same basis as for *D. spectabilis*.

Juvenile. Deciduous PM4,pm4 are present and show some or considerable wear. M1-2,m1-2 show some wear. M3,m3 are either just erupted or not erupted yet, and may show slight wear in older juveniles (Fig. 13; a, a′, b, b′). M3 usually shows more wear than m3. The skull is fragile and its dorsal surface convex. The auditory bullae are opaque and rough. The interparietal is wide and the supraoccipital is evident in its whole length.

Immature. Deciduous PM4,pm4 have just been shed. In older immatures, the permanent PM4,pm4 and M3,m3 show slight wear while M1-2,m1-2 have more wear (Fig. 13; c, c′). At the end of this stage, any one of the teeth still shows evidence of enamel infoldings. The skull is, in most cases, convex, the bullae are still opaque and rough and the interparietal is long and narrow.

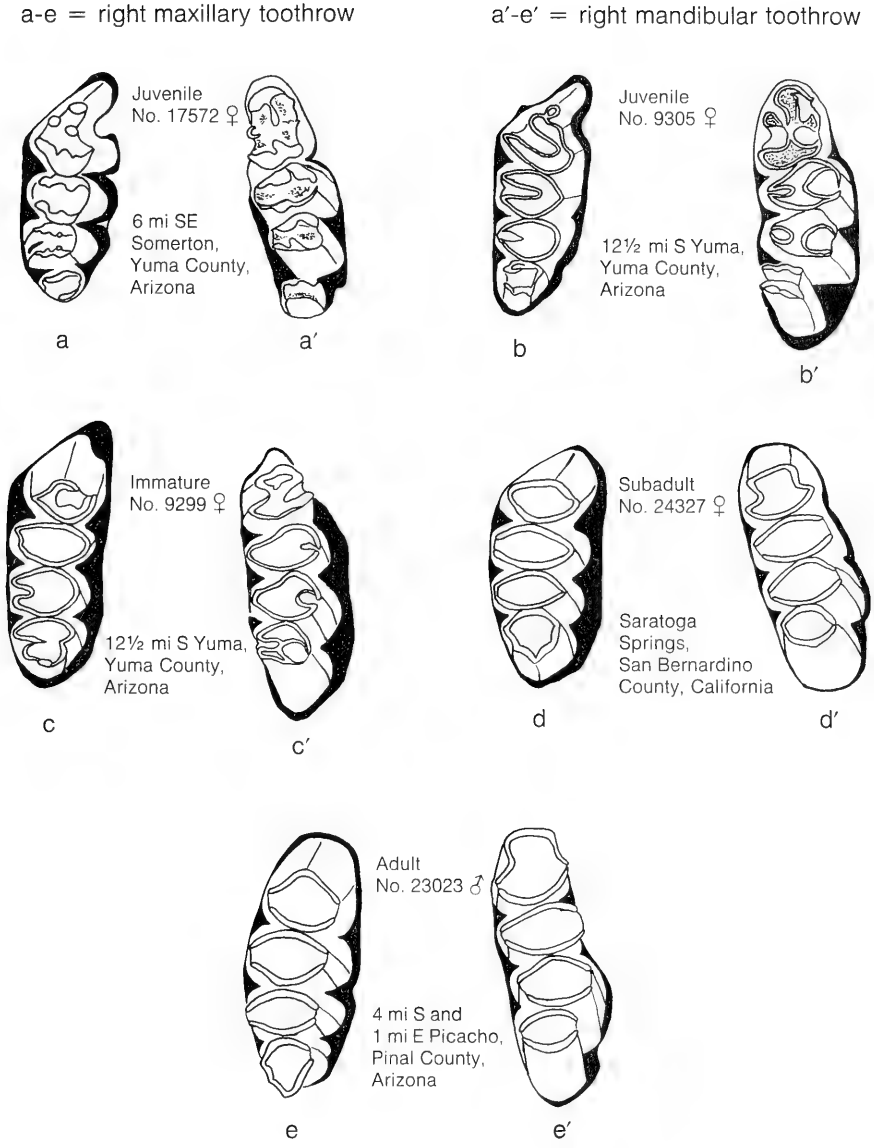


Fig. 13. Occlusal views of molariform teeth of different age groups of *Dipodomys deserti*. All specimens from UI Collection.

Subadult. All teeth show some wear. All molariform teeth except M3 and pm4 are almost oval in shape (Fig. 13; d, d′). M3 is usually pentagonal in shape with its apex directed posteriorly, while pm4 has two enamel infoldings, a deep lingual and a shallow labial. Enamel breaks develop in this stage and in some subadults all the teeth have them. The skull is slightly convex and the bullae are still rough and porous. The interparietal is usually absent and the supraoccipital is narrow.

Adult. All teeth show considerable wear (Fig. 13; e, e′). Enamel breaks are usually present in all teeth. The dorsal surface of the skull is flat and the bullae are shiny and translucent. The supraoccipital is narrow and in most cases is so restricted dorsally as to be absent.

The fur in the young individual is usually short and has more grayish color than that of the adult. The tail is covered with short hairs over its entire length. The dorsal and ventral tail stripes and the dark subterminal band of the tail are darker in young animals.

DENTITION

The sequence of tooth eruption in *D. deserti* is, in general, similar to that of *D. spectabilis.* In the youngest *D. deserti* examined, UI No. 17572 ♀, the deciduous PM4 has an anterior cusp, a protoloph, and a metaloph (Fig. 13 a). The two cusps of the protoloph are distinct, but none of the cusps of the metaloph is distinct. After some wear the two cusps of the protoloph unite with each other, then with the anterior cusp (Fig. 13 b). The protoloph later unites with the metaloph lingually, leaving a deep labial enamel infolding. The elongated deciduous pm4 has an anterior cusp, a protolophid, and a metalophid. The two cusps of the protolophid are distinct, but none of the cusps of the metalophid is evident (Fig. 13 b′). The anterior cusp unites first with the protolophid and later this unites with the metalophid at the middle of the occlusal surface, leaving two labial and two lingual enamel infoldings. When the occlusal surfaces of the deciduous PM4, pm4 are worn smooth, PM4 will have an almost triangular shape with its apex directed anteriorly and with no enamel infoldings, and pm4 will have a rounded anterior end and an almost straight posterior one. The two lophs of the permanent PM4 unite labially, leaving a deep lingual enamel infolding; while the two lophids of the permanent pm4 unite in the middle, leaving two deep enamel infoldings, one lingual and one labial (Fig. 13; c, c′). The protoloph and metaloph of M1-3 unite lingually leaving a deep labial enamel infolding (Fig. 13b). More-

over, in M3 there is a small indentation on the lingual side. The protolophid and metalophid of m1-3 unite in the middle of the tooth forming an H pattern and leaving deep labial and shallow lingual enamel infoldings (Fig. 13; b′, c′). In *D. deserti* in the immature age-group, the labial infoldings in the upper molars disappear in succession from the first to third molar. In the lower molars, the lingual infoldings disappear before the labial ones. The labial infoldings disappear in the same age-group and in the same sequence as in the upper molars.

All molariform teeth in the subadults are almost oval in shape except M3 and pm4 (Fig. 13; d, d′). The former is usually pentagonal in shape with its apex directed posteriorly while pm4 is squarish, but indented laterally on both sides because of the two enamel infoldings. These infoldings usually disappear in old adults, or become quite shallow.

Enamel breaks develop early in this species. They develop in the subadult age-group, and in some old subadults all teeth have them. The sequence of the development of the enamel breaks is as follows: They develop first in M1-2,m1-2; then in the premolars, in PM4 before pm4; the last teeth to develop enamel breaks are the third molars where they develop in m3 before M3. In old subadults all molariform teeth may have enamel breaks. These enamel breaks develop sometimes on the lingual side first, or on both sides at the same time. In pm4 of some old adults, two additional enamel breaks develop anterolaterally, one on each side. Enamel breaks disappear in some teeth in some old adults.

No groove in the anterior face of the lower incisors was found in any specimen.

Individual Variation

To analyze the individual variation in *Dipodomys deserti,* a grouped locality was formed from the southwestern corner of Yuma County, Arizona. This locality included specimens from: 7 mi S Yuma; 12 mi S Yuma; 6 mi SE Somerton; 5 mi ESE Somerton; 10 mi E and 4 mi S Yuma; and 3 mi E Somerton. A total of 32 adults, 18 males and 14 females was examined.

As in *D. spectabilis,* the 20 measurements studied in this species show normal variability except the least supraoccipital breadth and the distal white of the tail (Table 9). The greater inflation of the bullae in *D. deserti* reduces even more the size of the supraoccipital

TABLE 9

Coefficients of variation within a grouped locality of *Dipodomys deserti*, vicinity of Yuma, Yuma County, Arizona
(Superscript for number of specimens)

Character	18 ♂ ♂	14 ♀ ♀
Total length	5.50	3.69
Tail length	7.00	4.50
Hind foot length	3.53	2.88
Ear length	5.60[17]	6.89
Body length	4.95	4.35
Greatest skull length	2.80[11]	1.97[13]
Basal skull length	3.15[12]	2.27[12]
Length of nasals	4.25[17]	2.75
Breadth across maxillary arches	3.94[17]	3.24
Least interorbital breadth	4.61[10]	2.67[10]
Greatest breadth across bullae	2.62[15]	2.53[13]
Rostral breadth	5.23	3.25
Rostral depth	4.06	4.19
Bullar depth	2.76[12]	1.87[13]
Alveolar length of maxillary toothrow	3.48	4.34
Least breadth supraoccipital	124.92[16]	83.15[13]
Breadth across exoccipitals	3.38[11]	5.26[11]
Alveolar length of mandibular toothrow	4.63	3.57
Mandibular length	2.76	1.68
Length of white tip of tail	48.34	30.12[13]

and the interparietal, in comparison with *D. spectabilis*. The interparietal is usually absent in adult specimens and, when present, only a small part, its anterior end, is evident between the reduced arms of the supraoccipital. The supraoccipital dorsally appears to be absent but may remain as a narrow, splintlike bone that may widen out slightly at its anterior end. As was indicated under Materials and Methods, the least supraoccipital breadth and the length of the white tip of the tail were not used in the analysis of the geographic variation.

Again as in *D. spectabilis*, the external measurements are slightly more variable than the cranial measurements. Tail length and ear length vary the most. Rostral breadth, rostral depth, breadth across the exoccipitals, and alveolar length of the mandibular toothrow are more variable than other cranial measurements. The most variable measurement among them is the breadth across the exoccipitals.

The mean of the alveolar length of the maxillary toothrow was compared with that of the mandibular toothrow in both sexes. In both

cases the alveoli of the mandibular toothrow were slightly longer than those of the maxillary, but the differences were not significant.

Secondary Sexual Dimorphism

Males are generally larger than females. To analyze this secondary sexual dimorphism, the same grouped locality used in the analysis of the individual variation was employed. The means of the 18 measurements used in this analysis were larger for the males (Table 10). However, only in the following measurements were the differences significant: Tail length, basal length, greatest length, breadth across the maxillary arches, least interorbital breadth, greatest breadth across the bullae, rostral depth, breadth across the exoccipitals, and the mandibular length. Accordingly, these measurements were analyzed separately for males and females in the analysis of geographic variation.

Geographical Variation

Morphological variation among different populations of *Dipodomys deserti* throughout the range of the species is not great. Several factors may account for this. First, throughout its entire range, *D. deserti* inhabits an almost uniform terrain—loose sandy soil. Second, no geographic barrier permits isolation and differentiation within the range of *D. deserti*. The only geographic feature which may represent a barrier is the Colorado River. This, however, does not seem to be an effective barrier, especially near its southern end where the river is shallow and its course has shifted back and forth several times in the past (Goldman, 1937:429). That populations along both sides of the river in its southern region are similar in most characters is a demonstration of the ineffectiveness of the river as a barrier in this region. Although some of the populations present along the two sides of the river in west central Arizona and southeastern California exhibit slight differences in some of the measurements, these differences are irregular and do not follow a uniform pattern. Third, it seems that *D. deserti* has achieved a high degree of specialization for the type of habitat it occupies, and probably the future will bring little change in the morphology of this species. This assumption would be true only if there would be no major change in the habitat which *D. deserti* occupies at the present time, and provided that the limits of tolerance of this species are narrow. It is difficult to speculate about change in habitat, but the narrow limits of tolerance of this species is exhibited by its restriction to a specific type of habitat.

TABLE 10

Comparison between adult male and adult female *Dipodomys deserti*, vicinity of Yuma, Yuma County, Arizona

(Number of individuals, mean, range, one standard deviation, and one standard error of the mean. Measurements in mm)

Character	18 ♂ ♂	14 ♀ ♀
Total length	342.87	327.92
	(315.0-368.0)	(307.0-347.0)
	18.847	12.099
	±4.443	±3.235
Tail length	201.43	189.92
	(181.0-225.0)	(177.0-205.0)
	14.059	8.553
	±3.314	±2.287
Hind foot length	54.5	52.89
	(52.0-58.0)	(51.0-56.0)
	1.925	1.522
	±.454	±.406
Ear length	17.28	17.25
	(15.0-19.0)	(16.0-19.0)
	.969	1.188
	±.235	±.317
Body length	141.4	138.0
	(132.5-156.0)	(129.0-146.0)
	7.001	6.0
	±1.65	±1.603
Greatest skull length	46.12	44.7
	(44.2-47.9)	(43.3-46.4)
	1.291	.88
	±.39	±.245
Basal skull length	31.75	30.68
	(30.0-33.2)	(29.6-32.0)
	1.002	.698
	±.289	±.202
Length of nasals	17.46^{17}	16.88
	(16.4-18.6)	(16.1-17.5)
	.742	.464
	±.18	±.124
Breadth across maxillary arches	23.94^{17}	22.97
	(22.2-25.7)	(22.0-24.7)
	.943	.743
	±.229	±.198
Least interorbital breadth	14.42^{10}	13.62^{10}
	(13.5-15.8)	(13.1-14.4)
	.664	.364
	±.211	±.116

Table 10 contd.

Character	18 ♂ ♂	14 ♀ ♀
Greatest breadth across bullae	30.5[15]	29.57[13]
	(28.9-31.6)	(28.5-31.1)
	.80	.747
	±.207	±.207
Rostral breadth	4.05	3.96
	(3.8-4.5)	(3.7-4.2)
	.212	.128
	±.05	±.034
Rostral depth	7.77	7.44
	(7.2-8.2)	(7.1-8.0)
	.315	.311
	±.074	±.083
Bullar depth	15.23[12]	14.92[13]
	(14.6-16.0)	(14.5-15.5)
	.42	.279
	±.121	±.078
Alveolar length of maxillary toothrow	6.26	6.11
	(5.8-6.8)	(5.5-6.5)
	.218	.265
	±.052	±.07
Breadth across exoccipitals	13.29[11]	12.35[11]
	(12.5-13.8)	(11.5-13.5)
	.449	.65
	±.135	±.196
Alveolar length of mandibular toothrow	6.31	6.17
	(6.0-7.1)	(5.8-6.5)
	.292	.221
	±.068	±.058
Mandibular length	18.79	18.21
	(17.8-19.7)	(17.8-18.7)
	.163	.306
	±.038	±.082

Among the external measurements, the most variable, geographically, are total length and body length; among the cranial measurements, greatest length, and greatest breadth across the bullae. The least variable measurements, geographically, are the length of hind foot, rostral width, breadth across maxillary arches, and basal length.

As was stated earlier, males are usually larger than females in all the characters studied. The differences, however, are significant in only 9 of the 18 measurements compared, and morphological variations are

more evident among males than among females. In several of the characters there is some evidence of clinal change from the northwestern part of the range of the species in northwestern Nevada to the southeastern parts in south central Arizona and west central Sonora. Specimens from Nevada are smaller than those from Arizona and Sonora.

Nasal length and rostral depth are among the characters that show evidence of clinal change. They are larger in the southeastern populations than in the central and northwestern ones. Rostral breadth, however, does not show much variation throughout the entire range of the species. It is thought that the lengthening of the nasals and deepening of the rostrum, which consequently enlarge the volume of the nasal passages, act as a cooling device for the air during inhalation, and, more important, during exhalation to help condense the moisture in the exhaled air. Condensation of water from the expired air would result in conserving considerable water which is exceedingly important for these animals, as they are not known to be dependent on free water in the wild. Thus, the increase in the volume of the nasal passages appears to be directly correlated with an increase in temperature and a decrease in humidity. Setzer (1949:503) reported a reverse trend in *D. ordii* with regard to the length of nasals and the width of rostrum where they decreased as the southern limits of the range were approached, and he suggested that this may be correlated with the mean annual relative humidity of the environment.

SUBSPECIES OF *DIPODOMYS DESERTI*

***Dipodomys deserti deserti* Stephens**

Dipodomys deserti Stephens, Am. Naturalist 21:42, January 1887, original description.

Dipodomys deserti helleri Elliot, Field Columbian Museum, Publ. 87, Zool. Ser., 3:249, 7 January 1903, type: Male, adult skin and skull; No. 13007, Chicago Natural History Museum; from Keeler, Owens Lake, Inyo County, California; collected by E. Heller, 3 June 1903.

Dipodomys deserti deserti: Miller, U. S. Natl. Museum Bull., 79:277, 31 December 1912.

Type. Female, immature, skin and skull; No. 15629/22522, U. S. Biological Surveys Collection: from Mojave River, California [Mojave River bottom at "upper crossing" on old road from Cajon Pass to Rabbit Springs, 3 or 4 miles from, and opposite, Hesperia, San Bernardino County, California (Grinnell, 1922:108)]; obtained by Frank Stephens, 29 June 1886, original number 314.

Range. West central and southern Nevada, east central and southeastern California, northeastern Baja California, extreme southwestern Utah, western and southwestern Arizona, and northwestern Sonora. Limits of the range are fairly well known.

More specifically, in west central Nevada, from the vicinity of Wadsworth, Washoe County, to the Carson Sink area, south along the Walker River to the Huntoon Valley, Mineral County, east to San Antonio and Ralston Valley, south to 25 miles north of Ash Meadows and thence east to the western side of Beaver Dam Wash, Washington County, Utah. In east central California, from Oasis, Mono County, south to Saline Valley, Lone Pine, and Olancha, Inyo County, to the vicinity of Inyokern, San Bernardino County, to the vicinity of Neenach and east to Llano, Los Angeles County, to Agua Caliente and

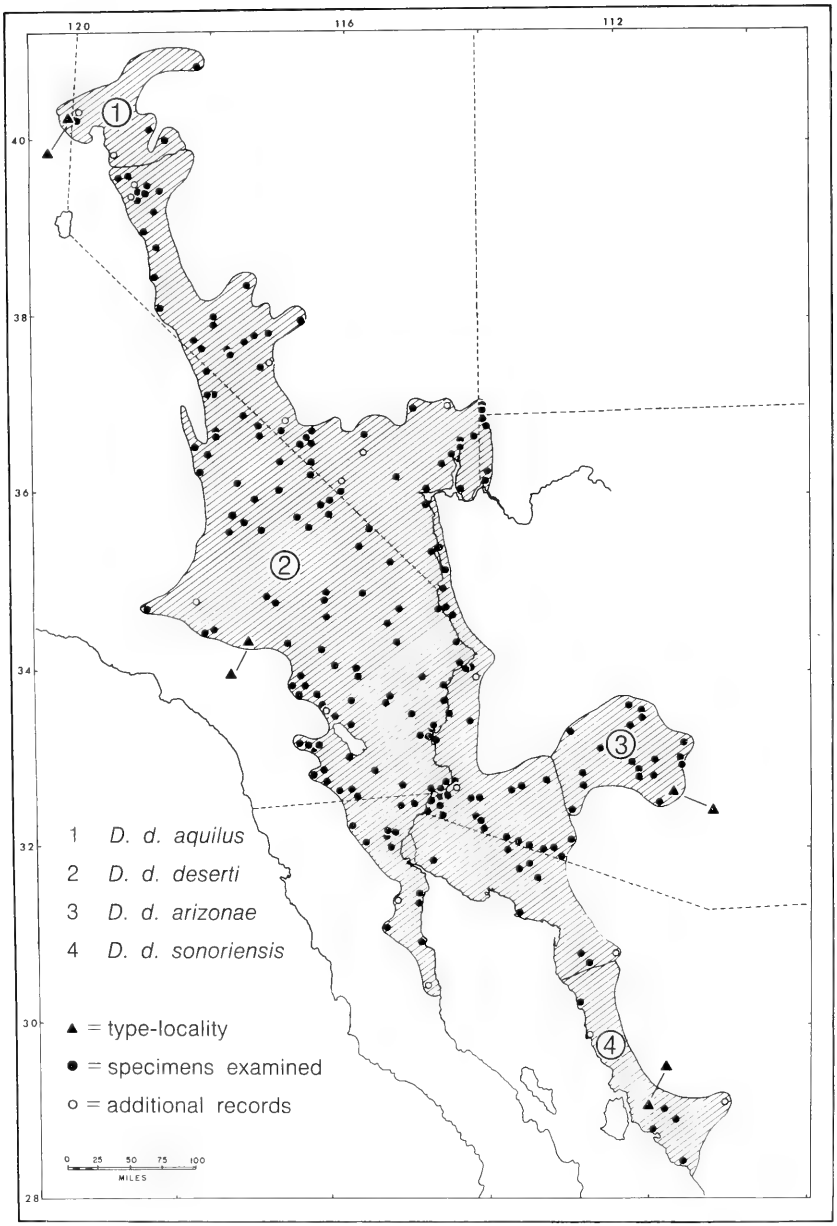


Fig. 14. Known occurrences and probable geographic range of the subspecies of *Dipodomys deserti* (*aquilus, deserti, arizonae, sonoriensis*).

Manson Valley, San Diego County. In Baja California, along the western edge of Laguna Salada and the eastern slopes of Sierra de Juárez and Sierra San Pedro Mártir to about 56 km south of San Felipe. In Arizona, along the northwestern border, south to Lake Mead, then along the eastern valley of the Colorado River south of Lake Mead to the vicinity of Bouse and Quartzsite, Yuma County, east along the Gila River to the vicinity of Sentinel, Maricopa County, south to Bates Well and Quitobaquito. In Sonora along the coastal area south to about the Río Magdalena.

Diagnosis.

Size: Large; adult total length 337.3 to 348.5 mm; tail length in males 197.0 to 211.7 mm, and in females 188.0 to 200.0 mm; body length 135.0 to 145.0 mm.

Color: In general, Light Buff to Pale Ochraceous-Buff, purest on sides, lightly mixed with long dusky hairs on dorsum; arietiform markings usually pale with distinct buffy spot at base of vibrissae; orbital ring dusky; small light buffy patch on outer side of leg usually extends to ankle; plantar stripe not too distinct; heel usually dusky or light brownish; ventral surface of toes white or washed with light yellowish color; dorsal tail stripe similar to color of dorsum or dusky; ventral tail stripe usually absent and if present narrow and broken with same color as dorsal stripe; subterminal band of tail dusky drab to dusky, usually not continuous all around.

Skull: Medium-sized; greatest length in males 45.1 to 46.3 mm, and in females 44.1 to 45.7 mm; rostrum shallow and usually slender; nasal length 16.4 to 17.1 mm; maxillary arch slightly slanted posteriorly, its posterolateral edge not flared out; breadth across maxillary arches 23.6 to 24.8 mm; least interorbital breadth small, in males 13.5 to 14.4 mm and in females 13.1 to 14.1 mm; lacrimal usually small; breadth across auditory bullae in males 30.1 to 30.9 mm and in females 29.5 to 30.5 mm; alveolar length of maxillary toothrow 5.6 to 6.0 mm; jugals usually heavy; mandibular length in males 18.2 to 18.9 mm and in females 17.5 to 18.8 mm. Also see Table 11.

Comparisons. Compared with *Dipodomys deserti aquilus, D. d. deserti* differs in the following: Size usually larger, especially in total length, tail length, and body length; color of upper parts, arietiform markings, plantar stripe, and dorsal tail stripe paler; ventral tail stripe usually absent; skull larger, particularly in greatest length, maxillary breadth, nasal length, and greatest breadth across the auditory bullae; incisors usually narrower.

TABLE 11

Measurements (in mm) of adult specimens representing the different subspecies of *Didopomys deserti*

(Mean with sample size as superscript and range below)

Character	*deserti* 8♂♂, 6♀♀	*aquilus* 2♂♂, 1♀	*arizonae* 13♂♂, 10♀♀	*sonoriensis* 7♂♂, 8♀♀
Total length	342.0^{14}	326.3^{3}	344.7^{21}	362.8^{15}
	313.0 — 376.0	325.0 — 328.0	325.0 — 361.0	345.0 — 385.0
Tail length	206.3^{14}	192.0^{3}	200.9^{21}	210.7^{15}
	187.0 — 229.0	190.0 — 195.0	190.0 — 310.0	198.0 — 231.0
Hind foot length	53.5^{14}	52.0^{3}	52.4^{23}	53.1^{15}
	51.0 — 56.0	51.0 — 53.0	49.0 — 56.0	52.0 — 55.0
Ear length	—	16.7^{3}	17.5^{15}	18.8^{15}
		16.0 — 17.0	16.0 — 19.0	18.0 — 20.0
Body length	137.2^{14}	134.3^{3}	143.9^{23}	152.1^{15}
	122.0 — 153.0	130.0 — 138.0	133.0 — 152.0	142.0 — 176.0
Greatest skull length	45.5^{11}	44.2^{3}	46.0^{20}	46.7^{14}
	44.5 — 46.5	44.0 — 44.3	44.1 — 48.1	45.6 — 47.8
Basal skull length	31.5^{11}	31.1^{3}	32.1^{19}	32.2^{14}
	30.8 — 32.2	30.5 — 31.6	30.7 — 34.1	31.7 — 32.6
Length of nasals	16.8^{11}	16.5^{3}	17.3^{23}	17.4^{14}
	16.1 — 17.5	16.1 — 16.7	16.1 — 18.4	16.2 — 18.6
Breadth across maxillary arches	23.3^{11}	22.6^{3}	23.5^{22}	24.6^{15}
	22.1 — 25.0	22.3 — 23.0	22.1 — 25.0	23.3 — 25.9
Least interorbital breadth	13.7^{11}	13.5^{3}	13.9^{22}	14.9^{15}
	13.2 — 14.5	13.1 — 13.8	12.8 — 15.4	14.2 — 15.7
Greatest breadth across bullae	30.2^{14}	29.5^{3}	30.9^{19}	31.1^{15}
	28.9 — 31.4	29.4 — 29.6	29.4 — 32.1	30.3 — 32.1
Rostral breadth	4.0^{14}	3.9^{3}	4.2^{23}	4.4^{14}
	3.7 — 4.3	3.7 — 4.1	3.9 — 4.5	4.1 — 4.7
Rostral depth	7.7^{14}	7.7^{3}	8.0^{23}	8.1^{15}
	7.3 — 8.3	7.6 — 7.8	7.7 — 8.8	7.8 — 8.4
Bullar depth	15.0^{14}	14.8^{3}	15.2^{19}	15.6^{15}
	14.5 — 16.1	14.8 — 14.8	14.6 — 15.8	15.2 — 16.1
Alveolar length max. toothrow	6.2^{14}	5.7^{3}	6.2^{23}	6.0^{15}
	5.8 — 6.5	5.5 — 6.0	5.8 — 6.8	5.6 — 6.4
Least breadth supraoccipital	0.2^{14}	0.6^{3}	0.4^{23}	0.4^{15}
	0.0 — 0.7	0.6 — 0.6	0.0 — 1.2	0.0 — 0.9
Breadth across exoccipitals	12.6^{12}	12.1^{3}	13.3^{19}	14.2^{14}
	11.7 — 13.8	11.6 — 12.3	12.4 — 14.4	13.5 — 14.8
Alveolar length man. toothrow	6.0^{14}	6.0^{3}	6.2^{23}	6.1^{15}
	5.7 — 6.2	5.8 — 6.2	5.9 — 6.8	5.7 — 6.5
Mandibular length	18.5^{14}	18.2^{3}	18.8^{23}	18.8^{15}
	17.9 — 19.9	17.9 — 18.8	17.5 — 19.9	17.9 — 19.7
Length white tip of tail	20.8^{8}	14.3^{3}	24.2^{20}	37.5^{13}
	12.0 — 30.0	10.0 — 18.0	15.0 — 36.0	18.0 — 66.0
Weight, grams	118.3^{1}	113.4^{3}	—	129.5^{3}
		110.7 — 115.7		116.0 — 137.0

deserti: Palm Springs, Riverside County, California
aquilus: 21 mi W, 2 mi N Lovelock, Pershing County, Nevada
arizonae: 3 mi SE Picacho; 4 mi S, 1 mi E Picacho, Pinal County, Arizona
sonoriensis: 1 mi N Rancho de Costa Rica; Rancho de Costa Rica, Sonora

Compared with *Dipodomys deserti arizonae*, *D. d. deserti* differs in the following: Size usually smaller, especially body length; color of upper parts paler, less mixed with blackish and grayish hairs; arietiform markings and dorsal tail stripe paler; ventral tail stripe usually absent; plantar stripe paler or absent; subterminal dark band of tail paler; skull smaller in general; basal length smaller; rostrum shallower; maxillary arches more slanted posteriorly; mastoidal bullae usually less inflated; greatest breadth across the bullae and mandibular length smaller.

Compared with *Dipodomys deserti sonoriensis*, *D. d. deserti* differs in the following: Total length, tail length, and body length smaller; color of upper parts paler, less mixed with blackish hairs; arietiform markings and dorsal tail stripe paler; ventral tail stripe usually absent; plantar stripe paler or absent; subterminal dark band of tail paler; skull smaller in general, especially in greatest length and in greatest width across auditory bullae; maxillary arches heavier; rostrum usually shallower; lacrimal smaller; jugal heavier; mastoidal bullae less inflated; bullar depth, interparietal width, and alveolar length of maxillary toothrow smaller.

Remarks. Typical *Dipodomys deserti deserti* is characterized by its pale buff color, pale arietiform markings, and the absence of a dark ventral tail stripe. The skull is medium-sized, but the posterolateral edges of the maxillary arches are not flared out and the auditory bullae are medium in size.

Dipodomys deserti deserti intergrades, in a wide zone, with *D. d. arizonae* in southwestern Arizona. Some specimens from the following localities have some external and cranial characters in addition to some color features close to those of *D. d. arizonae*: Sentinel, Maricopa County; Bates Well, Pima County; northern bondary of Organ Pipe Cactus National Monument; 7 mi E Papago Well; 9 mi E Papago Well; Quitobaquito.

The zone of intergradation between *Dipodomys deserti deserti* and *D. d. sonoriensis* has not been clearly determined because of insufficient material from this area. These two subspecies may intergrade along the Río de Magdalena in northwestern Sonora. One adult from Est. Enchilayas has a larger body than *D. d. deserti* and in this respect is closer to *D. d. sonoriensis.*

Dipodomys deserti deserti intergrades with *D. d. aquilus* in northwestern Nevada. Several specimens from the vicinity of Wadsworth, Washoe County, and those from 6 mi NE Fernley, Lyon County, and some specimens from the vicinity of Fallon, Churchill County, are

smaller in some external and cranial measurements than typical *D. d. deserti*. The specimens from the vicinity of Fernley have a darkish color, closer to that of *D. d. aquilus*.

Color variation is apparent between different populations in this subspecies, especially those populations from southwestern Arizona. No appreciable skull differences, however, were found in these populations to warrant taxonomic recognition. The palest colored specimens are among the populations from southeastern California. The general color of the upper parts becomes more buffy (Pale Ochraceous-Buff) among populations from the western part of the range in California. In west central Nevada, the color becomes increasingly mixed with long dusky hairs, and the color markings become darker in the populations to the northwestern part of the range. Specimens from northwestern Arizona and the Beaver Dam Wash area in southwestern Utah have a slightly darker coloration and occasionally a disrupted or broken ventral tail stripe is observed. Specimens from Baja California have a more buffy tone than those from southeastern California. The buffiest specimens of this race are found in southwestern Arizona, especially in the Yuma-Somerton area, and in northwestern Sonora. The color of these specimens is Light Ochraceous-Buff with a slightly pinkish cast, occasionally mixed with long dusky hairs and the subterminal band of the tail is usually dusky. The long dusky hairs are quite prominent in specimens from Punta Peñasco, Sonora.

The type-specimen of this subspecies is an immature with the permanent PM4, pm4 erupted but almost unworn. Also a narrow interparietal bone is present in this specimen.

Specimens from several isolated and noncontiguous populations of *D. d. deserti* have skulls larger in several measurements than those from the type locality. Such populations are found in Llano, Los Angeles County, California; the vicinity of San Felipe, Baja California; Wellton, Yuma County; and Quitobaquito, Pima County, Arizona. These represent variable populations and are not of a subspecific importance.

Three specimens from Oasis, Mono County, represent a new county record for the state of California for *D. d. deserti*.

Limits of the range of this subspecies are fairly well known and future collecting is unlikely to reveal any significant range extension. *D. d. deserti* is occupying, at the present time, almost all the suitable desert habitat in southwestern North America.

Specimens examined. A total of 1,307 specimens from:

NEVADA. Washoe County: 1 mi W Wadsworth, 1 (MVZ); ¼ mi E

Wadsworth, 1 (MVZ). LYON COUNTY: 6 mi NE Fernley, 2 (MVZ); ½ mi SE Wadsworth, 4,200 ft, 1 (MVZ); 1 mi SE Wadsworth, 4,200 ft, 1 (MVZ). CHURCHILL COUNTY: 10 mi NW Fallon, 1 (USNM); 7 mi NW Fallon, 4,000 ft, 1 (USNM); 1 mi NW Soda Lake, 4,000 ft, 2 (KU), 1 (MVZ); 1 mi S Soda Lake, 4,000 ft, 1 (MVZ); 4 mi NW Fallon, 4,000 ft, 2 (USNM); 4 mi NE Fallon, 1 (UI); 7 mi W Fallon, 7 (UI); 5 mi W Fallon, 4,000 ft, 1 (MVZ); 4 mi W Fallon, 4,000 ft, 2 (MVZ); Ragtown, Carson River, 4 (USNM); 14 mi WSW Fallon, 13 (KU); 8 mi S Soda Lake, 4,000 ft, 1 (MVZ); 16 mi S Fallon, 2 (KU). MINERAL COUNTY: 8 mi NNW Schurz, Walker River, 2 (KU); 8 mi SE Schurz, 4,100 ft, 1 (MVZ); Cat Creek, 4 mi W Hawthorne, 4,500 ft, 1 (MVZ); Huntoon Valley, 5,700 ft, 4 (MVZ). ESMERALDA COUNTY: Columbus, 3 (USNM); 3½ mi SE Coaldale, 4,850 ft, 2 (MVZ); 4 mi SE Coaldale, 4,850 ft, 2 (KU), 2 (MVZ); 13 mi N Goldfield, 5,100 ft, 1 (MVZ); 13½ mi NW Goldfield, 4,850 ft, 13 (MVZ); 7 mi N Arlemont, 5,500 ft, 17 (MVZ); 1 mi S Fish Lake, 1 (MVZ); Clayton Valley, 5 mi SE Blair, 5,000 ft, 1 (USNM); 8 mi SE Blair, 4,500 ft, 3 (MVZ); Clayton Valley, sand dunes, 8 mi SE Blair, 4,000–4,500 ft, 6 (USNM). NYE COUNTY: San Antonia, 5,400 ft, 1 (MVZ); Ralston Valley, 5,650 ft, 34 mi E, 1 mi N Tonopah, 1 (MVZ); N shore Mud Lake, 5,300 ft, S end Ralston Valley, 2 (MVZ); Thorpes [=Thorps Mill], 4 (USNM); Oasis Valley, 1 (USNM); Table Mt., 25 mi N Ash Meadows, 4 (USNM); 20 mi NNW Ash Meadows, 2 (USNM); Amargosa Desert, 2,500 ft, 20 mi SE Beatty, 4 (MVZ); 15 mi N Ash Meadows, 3 (USNM); Ash Meadows, 38 (USNM); Pahrump Valley (near Stewart Well), 16 (USNM). LINCOLN COUNTY: Coyote Spring, 2,800 ft, 4 (MVZ), 1 (SDSNH). CLARK COUNTY: Indian Spring Valley, 14 mi N Indian Springs, 3,100 ft, 1 (CAS), 11 (MVZ); Bunkerville (Virgin River Valley), 2 (USNM); 7 mi N [on] Virgin arm of Boulder Lake [=Lake Mead], E side, 920 ft, 1 (MVZ); 5 mi SE Overton, 1,200 ft, 1 (MVZ); island in Boulder Lake, mouth of Virgin River, 1 (MVZ); Valley of Fire, 12 mi SW Overton, 1 (MVZ); 1½ mi NW Corn Creek Hdq., Desert Game Ranch, 1 (USNM); Corn Creek Ranch, 1 (USNM); Colorado River, bend near Calville (orig. tag: Lincoln Co.), 1 (USNM); Colorado River (orig. tag: Lincoln Co.), 4 (USNM); Stone's Ferry, 1 (USNM); Colorado River Head of Black Cañon (orig. tag: Lincoln Co.), 1 (USNM); Colorado River at Jap Ranch, 14 mi E Searchlight, 500+ ft, 12 (MVZ).

CALIFORNIA. MONO COUNTY: Oasis, 3 (LACM). INYO COUNTY: Owens Valley, 6 mi S Alvord, 4,000 ft, 2 (USNM); Big Sand Dunes, Eureka Valley, 300 ft, 3 (MVZ); Mesquite Spring, N end Death Valley, 6 (SDSNH); Death Valley, Mesquite Valley, 3 (USNM); Death Valley,

Mesquite Well, 4 (USNM); Mesquite Flat, 8 mi N Stovepipe Wells, Death Valley, 2 (SDSNH); 3 mi N Saline Valley, Soda Works, 1,140 ft, 2 (MVZ); Midway Well, Death Valley National Mon., 1 (CAS); Saline Valley, Soda Works, 1,100 ft, 1 (MVZ); Triangle Spring, Death Valley, −13 ft, 1 (LACM), 6 (MVZ); Salt Creek, Death Valley, −200 ft [SE corner of T15S, R45E], 2 (MVZ); Lone Pine, 5 (USNM); 4 mi N Keeler, 6 (SDSNH); Keeler, ½ mi [E] from Lake, 2 (MVZ); Keeler, 3,600–3,604 ft, 5 (FMNH), 37 (MVZ), 12 (USNM); 1.2 mi (by road) SSE Keeler, 3,600± ft, 6 (MVZ); Furnace Creek Ranch, Death Valley, −178 ft, 34 (MVZ); Furnace Creek (Death Valley), 7 (FMNH), 23 (USNM); 2 mi S Furnace Creek Ranch, Death Valley, −178 ft, 1 (MVZ); 3 7/10 mi NE Olancha, Sanddune, 3,600 ft, 4 (MVZ); Kelley's Well, Amargosa River, 2,100 ft, 3 (MVZ); Death Valley, 6 (AMNH), 1 (KU), 23 (USNM); Panamint Valley, 11 (USNM); Bennett's Wells, Death Valley, 18 (USNM); Ballarat, 2 (FMNH); 12 miles Spring, near Resting Springs, 8 (USNM); Shoshone, 10 mi W of Kingston Ranch, 1,560 ft (T22N, R7E), 2 (MVZ); Resting Springs, Death Valley, 8 (USNM); Argus Mt., 2,200 ft, 2 (USNM); Amargosa River, 1 (USNM); Amargosa Valley, 4 (USNM); Amargosa, 3 (USNM); Amargosa Wash, S end Death Valley, 1 (USNM).

Los Angeles County: 2 mi S Pecks Butte, Mojave Desert, 2,650 ft, 6 (MVZ); Black Butte, Mojave Desert, 3,000 ft, 1 (MVZ); Llano, 1 (CAS), 16 (LACM).

San Bernardino County: Borax Flat, 1,750–2,100 ft, 5 (USNM); Saratoga Spring, 1 (LACM), 1 (UI), 8 (USNM); 8½ mi SSE Ripley (Nevada) [about 5 mi SE Kingston], 14 (MVZ); Lone Willow Spring, 7 (USNM); 15 mi E Inyokern, 1 (MVZ); Raymond's Well, Salt Well Valley, 2,500 ft [plotted as Salt Well], 5 (USNM); 8 mi W Clark Mt., 3,300 ft, 2 (MVZ); Ivanpah, 2 (USNM); Mesquite, 1,246 ft, 1 (MVZ); 2½ mi SW Kelso, 2,100 ft, 20 (MVZ); 1½ mi NE Barstow, Mojave Desert, 2,200 ft, 3 (MVZ); Afton Canyon, Mojave Desert, 44 mi E Barstow, 1 (MVZ); Daggett, 23 (FMNH); Fenner, 2,000 ft, 1 (USNM); Needles, 1 (CAS); Ludlow, 1,712 ft, 2 (AMNH), 1 (MVZ), 9 (USNM); Danby, 1,500 ft, 2 (USNM); Hesperia, 1 (USNM); Mojave River, 8 (USNM); Cottonwood Spring, 1 mi W Old Woman Springs, 3 (MVZ); 7½ mi NE Chubbuck, Old Woman Mts., 2,320 ft, 1 (MVZ); Colorado River, 29 mi S Needles, 5 (KU); Surprise Spring (T3N, R7E), 35 mi NE Whitewater Station, 2,400 ft, 1 (MVZ); 4 mi N Twentynine Palms, 2,200 ft, 1 (MVZ); 16 mi E Twentynine Palms, 1 (MVZ); Colorado River, opp. Parker [Arizona], 350 ft, 1 (USNM); Mojave Desert, E Morong [=Morongo] Valley, 3,100 ft, 2 (USNM); 1 mi S Virginia Dale mine, Joshua

Tree National Monument, 1,900 ft, 1 (MVZ); 2 mi S Blythe Jct. [=Rice], 800 ft, 1 (MVZ).

RIVERSIDE COUNTY: Seven Palms [Well], 1 (CAS); White Water [=Whitewater], near San Jacinto Mts. (orig tag: San Diego Co.), 1 (AMNH), 1 (FMNH), 1 (SDSNH), 1 (USNM); Whitewater Station, 1,130 ft, 6 (MVZ); Riverside Mt., Colorado River, 1 (MVZ); 1,000 Palms, 2,000 ft, 2 (MVZ); Palm Springs, 455 ft, Colorado Desert, 4 (FMNH), 2 (LACM), 8 (MVZ), 2 (SDSNH), 2 (USNM); 1 mi S Palm Springs, 1 (MVZ); S end Coxcomb Mts., 1 (LACM), 1 (UI); 1¼ mi W, 2¾ mi S Pinto Peak [in the Joshua Tree National Monument], 1,775 ft, 3 (MVZ); Indio, 1 (USNM); 4 mi NE Desert Center, 1 (LACM); 3 mi N Palo Verde intake, 300 ft, Colorado River, 1 (LACM); 4 mi NE Mecca, 1 (MVZ); Hopkins Well, 2 (LACM), 1 (UI); Mecca, 36 (MVZ); Dos Palmos (2 mi W Dos Palmos Spring), 2 (MVZ); 15 mi SW Ehrenberg, 2 (USNM); Rannels [=Rannells] (orig. tag: Imperial Co.), 4 (LACM).

SAN DIEGO COUNTY: Aqua Caliente, Colorado Desert, 1 (AMNH), 1 (USNM); Baregas [=Borrego] Springs, 5 (AMNH), 4 (FMNH), 3 (USNM); Borego [=Borrego] Valley, 4 (SDSNH); Borego [=Borrego] Hotel, 3 (CAS); San Felipe Narrows, 1 (LACM); La Puerta Valley [=Manson Valley], 2,100 ft, 10 (SDSNH); Carrizo Creek, 500 ft, 1 (LACM), 3 (MVZ), 3 (SDSNH).

IMPERIAL COUNTY: Palo Verde, 2 (LACM); 25 mi SW Ehrenberg, 1 (USNM); 4 mi S Palo Verde, 275 ft, 5 (AMNH), 2 (MVZ); Salt Creek, 2 (MVZ); Brawley, 3 (USNM); 15 mi E Holtville, 3 (SDSNH); Laguna, Colorado Desert, 1 (FMNH), 2 (SDSNH); Indian Wells, New River (orig. tag: San Diego Co.), 2 (AMNH), 1 (USNM); Coyote Well, 4 (MVZ); Coyote Wells, Colorado Desert, 1 (USNM); Coyote Wells, 271 ft, 4 (CAS), 1 (SDSNH), 1 (USNM); 1 mi W Pilot Knob, 1 (SDSNH); Pilot Knob (orig. tag: San Diego Co.), 1 (USNM); Pilot Knob, Colorado River, 2 (MVZ); near Pilot Knob, Colorado River, 6 (MVZ); Fort Yuma, 3 (LACM); 14 mi W Calexico, 1 (MVZ).

BAJA CALIFORNIA. Alamo River, 20 mi SW Pilot Knob, 50 ft, 12 (MVZ); Gardner's Laguna, Salton River, 2 (USNM); Las Palmas Canyon, W side of Laguna Salada, 15 mi S of N end, 200 ft, 2 (MVZ); Volcano Lake, 5 (USNM); 13 mi N El Mayor, 2 (MVZ); Base Cocopah Mts., 100 ft, 1 (USNM); De Mara's Well (on W side of) Laguna Salada [35 mi below International Line (Huey, 1951:253)], 5 (SDSNH); Mount Mayor, 1 (USNM); 40 mi N San Felipe, 1 (SDSNH); 36 mi N San Felipe, 1 (LACM); 30 mi N San Felipe, 1 (SDSNH); Valley at E base, San Pedro Martir Mts., 5 (USNM); San Felipe, 11 (FMNH), 15 (MVZ),

9 (SDSNH); San Felipe Bay, 3 (USNM); Sonora del Norte, 3 mi SSW San Felipe, 4 (MVZ).

UTAH. WASHINGTON COUNTY: Beaver Dam Wash, 8 mi N Utah-Arizona border, 2,600–2,800 ft, 2 (UU); ½ to ¼ mi S Terry's Ranch on Beaver Dam Wash, 7 to 6¾ mi N Utah-Arizona border, 2,600 ft, 1 (UU); Beaver Dam Wash, 5 mi N Utah-Arizona border, 2,600 ft, 6 (UU); Beaver Dam Wash, 1 (UI).

ARIZONA. MOHAVE COUNTY: Mormon Well, Beaver Dam Wash, 1 (KU); near mouth of Beaver Dam Creek, just above Littlefield, 1,500 ft, 7 (USNM); Littlefield, 1,500 ft, 1 (USNM); Beaver Dam (Lodge), 1,900 ft, 14 (UI); Beaver Dam (Nevada) [in the Virgin River Valley], 1 (USNM); Grand Wash, 2,100 ft, 2 mi S, 3 mi E Pakoon Springs, 3 (UI); Black Willow Spring, 1,900 ft, 4 mi S of Pakoon Springs, 5 (UI); Seven Springs, 1,600 ft, 8 mi S, 1 mi W Pakoon Springs, 9 (UI); Grand Wash, 1,800 ft, 8 mi S Pakoon Springs, 1 (USNM); Lake Mead, 1,200 ft, foot of Grand Wash, 4 (UI); Old Searchlight Ferry, 500± ft, 8 (MVZ); Old Searchlight Ferry, Colorado River, 1,000 ft, 1 (USNM); Colorado River, 31 mi N, 2½ mi W Camp Mohave, 5 (MVZ); Harper's Ferry, 7 (USNM); Fort Mohave, 13 (USNM); opposite Needles, Wm. Robert's Ranch, 500 ft, 1 (USNM); Mellen [=Topock], 18 (MVZ); Topock, 600 ft, 2 (USNM). YUMA COUNTY: Parker, 350 ft, 8 (USNM); 5 mi E Parker, 4 (KU); 5½ mi E Parker, 9 (UI); 5½ mi SE Parker [actually 5 mi E], 1 (UI); Ehrenberg, 2 (LACM), 1 (USNM); Ehrenberg, Colorado River, 2 (MVZ); 10 mi S Quartzsite, 1 (LACM); 25 mi below Ehrenberg, Colorado River, 1 (MVZ); 15 mi NE Yuma, 3 (USNM); 5 mi NE Laguna, Colorado River, 3 (MVZ); Dateland, 5 (FMNH); Texas Hill [=Stoval], 2 (USNM); 6 mi E Yuma, 1 (SDSNH); Yuma, 13 (USNM); Old Quarry near Yuma, 1 (SDSNH); near Yuma, 4 (FMNH); 2½ mi SE Yuma, 1 (MVZ); 10 mi E, 4 mi S Yuma, 1 (UI); Gila Center, 5 (USNM); Adonde, 11 (USNM); ½ mi E Wellton, 3 (UI); Wellton, 20 (SDSNH), 2 (USNM); 9 mi SW Yuma, 2 (MVZ); 7 mi S Yuma, 1 (UI); 3 mi E Somerton, 8 (UI); 12½ mi S Yuma, 11 (UI); 5 mi ESE Somerton, 6 (UI); 6 mi SE Somerton, 20 (UI); 4 mi S Gadsden, 120 ft, 5 (AMNH), 8 (MVZ); Monument 204, Colorado River, 27 (USNM); 10 mi SE Fortuna Mine, 300 ft, 1 (MVZ); Yuma Desert, Monument 200, 3 (USNM); 16 mi SE Fortuna Mine, 300 ft, 5 (AMNH), 1 (KU), 11 (MVZ); Tinajas Altus [=Altas], 1 (USNM); Tule Wells, 1 (USNM); S end Tule Desert, 3 mi N Monument 182, 1 (SDSNH); E end Pinacate, 2 mi NW Monument 180, 6 (UI). PIMA COUNTY: Bates Well, 2 (MVZ); N Boundary Organ Pipe Cactus National Monument, 15 mi S Ajo, 5 (UI); Papago Well, 1 (UI); 7 mi E Papago Well, 2 (SDSNH); 9 mi E Papago Well, 1,100 ft, 1

(MVZ); Quitovaquito [=Quitobaquito], 1 (SDSNH), 7 (USNM). MARICOPA COUNTY: Sentinel, 2 (AMNH).

SONORA. S base Tule Mts., 3 (USMN); El Doctor, 5 (UCLA); ½ mi S Crater Elegante, 34 mi W Sonoita [=Sonoyta], 900± ft, 1 (MVZ); Poso McDougal, Pinacate Region, 850+ ft, 1 (MVZ); Batamote, Río Sonoita [=Sonoyta], 30 mi WSW Sonoita [=Sonoyta], 8 (MVZ); 1 mi NNE Punta Peñasco, 2 (MVZ); Punta Peñasco, 50+ ft, 1 (MVZ); Punta Peñascosa [=Peñasco], 17 (SDSNH); near Punta Peñasco, 1 (UNM); Est. (Las) Enchilayas, 2 (FMNH); 28 mi W Caborca, Vado El Coyote, 1 (UI).

Additional records. NEVADA. (All from Hall, 1946:431, unless otherwise indicated.) CHURCHILL COUNTY: 15 mi WNW Fallon, 1 (KU); 15 mi WSW Fallon, 1 (KU). NYE COUNTY: Stonewall Flat, 14 mi SE Goldfield; 1 mi N Beatty, 3,400 ft; 3½ mi N Pahrump, 2,667 ft; 1½ mi N Pahrump, 2,667 ft. LINCOLN COUNTY: Carp. CLARK COUNTY: Mesquite; Indian Springs, 3,280 ft; St. Thomas; ½ mi E St. Thomas; Corn Creek, 2,840 ft.

CALIFORNIA. LOS ANGELES COUNTY: 16 mi NE Palmdale, about 3,261 ft (Butterworth, 1961a). SAN BERNARDINO COUNTY: Calico Valley, 1 (Brattstrom, 1960:404). RIVERSIDE COUNTY: Coachella, 1 (Grinnell, 1922:110).

BAJA CALIFORNIA. 61 km NE, 3.4 km W San Felipe (Alvarez, 1960:422); 56 km S San Felipe (Alvarez, 1960:422).

ARIZONA. YUMA COUNTY: 11 mi NW Bouse, 1 (Cockrum, 1960: 154); 2 mi NE Ehrenburg, 1 (TCWC); 15 mi NE Yuma (Cockrum, 1960:154). PIMA COUNTY: SE Growler Valley, about 3 mi SW Growler Mine (Huey, 1942:361); 1 mi E Quitovaquita [=Quitobaquita], Abra Valley (Huey, 1942:361).

SONORA. Near Puerto Peñasco, 2 (UA, Cockrum and Bradshaw, 1963:8); Rancho Noce Buena Vieja, 120 km SE [12 km N *sic*] Sonoyta (Alvarez, 1960:422).

Dipodomys deserti aquilus Nader

Dipodomys deserti aquilus Nader, Proc. Biol. Soc. Washington, 78 (5): 52, 21 July 1965, original description.

Type. Male, adult, skin and skull; No. 126411, Museum of Vertebrate Zoology, University of California; from 1½ mile northwest High Rock Ranch, about 12 miles southeast of Wendel, 4,080 feet, Lassen County, California; obtained by C. S. Thaeler, 21 July 1960, original number 1022.

Range. East central Lassen County, California, and northwestern Nevada.

More specifically, from the vicinities of Wendel and High Rock Ranch, Lassen County, California, east to the vicinities of Nixon and Flanigan, Washoe County, Nevada, northeast to the vicinity of Jungo, Humboldt County, and southwest to Adobe Flat and the vicinity of Toulon, Pershing County. Limits of the range are not too well known, especially in the northern and northwestern parts; future collecting may reveal a wider range of this subspecies in these directions.

Diagnosis.

Size: Small, adult total length averages about 323.5 mm; tail length averages in males about 193.4 mm and in females about 190.0 mm; body length averages about 132.2 mm.

Color: In general, Pale Ochraceous-Buff, heavily mixed with grayish and long blackish hairs on dorsum; arietiform markings dusky; orbital ring blackish; plantar stripe brownish-black; dorsal tail stripe dark; ventral tail stripe dark and usually present; subterminal band of tail blackish.

Skull: Small-sized; greatest length averages about 44.2 mm; breadth across maxillary arches narrow, averaging 23.0 mm; nasals short, averaging 16.2 mm; greatest breadth across auditory bullae narrow, averaging about 29.5 mm; incisors robust. Also see Table 11.

Comparisons. For comparison with *Dipodomys deserti deserti*, see account of that subspecies (p. 83).

Remarks. Typical *Dipodomys deserti aquilus* is characterized by its small external measurements, dark color, and small skull, especially the greatest length, maxillary breadth, nasal length, and greatest breadth.

Dipodomys deserti aquilus intergrades with *D. d. deserti* in northwestern Nevada. Specimens from the vicinity of Toulon, Pershing County, Nevada, are slightly larger in some measurements than typical *D. d. aquilus*. Some of these specimens lack the ventral tail stripes.

An adult specimen from near High Rock Ranch, Lassen County, and the young specimens from near Flanigan, Washoe County, are darker than the other specimens from northwestern Nevada.

Specimens examined. A total of 12 specimens from:

CALIFORNIA. Lassen County: 1½ mi NW High Rock Ranch, T 28 N, R 17 E, Sec. 26, 4,040 ft, 1 (MVZ).

NEVADA. Washoe County: 4½ mi N, 4½ mi W Flanigan, 4,000±

Fig. 15. *Dipodomys deserti arizonae* from 4 mi S and 1 mi E Picacho, Pinal County, Arizona. (Photograph by W. Goodpaster)

ft, 2 (MVZ). HUMBOLDT COUNTY: 8 mi E, 1 mi N Jungo, 4,200 ft, 1 (MVZ). PERSHING COUNTY: 21 mi W, 2 mi N Lovelock, 4,000 ft, 3 (MVZ); 3¼ mi NNE Toulon, 3,900 ft, 1 (MVZ); 3 mi E Toulon, 3,900 ft, 4 (MVZ).

Additional records. NEVADA. WASHOE COUNTY: 16 mi E Wendel (California) (Hubbard, 1961:135); 4½ mi N and 2½ mi W Nixon, 2 (Coll. Ira W. La Rivers and T. J. Trelease) (Hall, 1946:431); ½ mi SE Pyramid Lake, 3 (Stock, 1974:506).

Dipodomys deserti arizonae Huey

Dipodomys deserti arizonae Huey, Trans. San Diego Soc. Nat. Hist., 12:99, 10 February 1955, original description.

Dipodomys deserti sonoriensis: Willet, J. Mammal., 18:101, 14 February 1937.

Type. Male, adult, skin and skull; No. 12532, San Diego Society of Natural History Collection; from 3 miles southeast of Picacho, Pinal County, Arizona; obtained by Laurence M. Huey, 14 May 1937, no original number.

Range. South central Arizona.

More specifically, north from about 10 mi N Sunnyslope, Maricopa County, Arizona, southeast to Florence Junction, south to the vicinity of Picacho and Green's Reservior, Pinal County, west to about 10 mi N Ajo, Pima County, north to about 15 mi NW Buckeye, Maricopa County. Limits of the range are fairly well known except in the western and the northwestern parts.

Diagnosis.

Size: Large.

Color: In general, Pale Ochraceous-Buff heavily mixed with grayish and long dusky hairs on dorsum; arietiform markings dusky to black; orbital ring dusky to blackish; plantar stripe light brown to dark brown; ventral side of toes usually yellowish; dorsal tail stripe blackish; dark ventral tail stripe continuous or broken; subterminal dark band of tail brown to blackish; usually meets ventrally at its distal end in a narrow zone.

Skull: Large-sized, adult basal length large, in males 32.4 to 33.1 mm and in females 30.5 to 32.2 mm; nasals usually long, 17.2 to 17.8 mm; lacrimal usually small; jugals usually heavy; maxillary arches more acutely angled with long axis of skull; anteromedial border of maxillaries extend somewhat along nasals; rostral depth in males 8.1 to 8.3 mm and in females 7.7 to 8.1 mm; mandible long, in males 19.0 to 19.4 mm and in females 18.0 to 19.1 mm. Also see Table 11.

Comparisons. Compared with *Dipodomys deserti sonoriensis, D. d. arizonae* differs in the following details: Color of upper parts slightly paler and more buffy; total length usually less; tail shorter; body usually shorter; skull with maxillary arches heavier, less slanted posteriorly, and their posterolateral edges less flared out; jugals heavier; lacrimals smaller; auditory bullae shallower; interorbital breadth usually narrower; mandible usually longer; alveolus of mandibular toothrow longer.

For comparison with *Dipodomys deserti deserti,* see account of that subspecies (pp. 85 ff.).

Remarks. Typical *Dipodomys deserti arizonae* is characterized by its grayish color, dark ventral tail stripe, large auditory bullae, more angled maxillary arches with reference to the long axis of the skull, alveoli of maxillary toothrow long, and long mandible.

In comparing *Dipodomys deserti arizonae* with *D. d. deserti,* Huey (1955:99) stated that the former has a smaller skull and a slenderer

rostrum. This study shows that topotypes and most *D. d. arizonae* are larger, in several cranial measurements, than those of *D. d. deserti* (also see Table 11). As for the slenderness of the rostrum, there are no real differences between the two subspecies, and in fact many specimens of *D. d. deserti* have slenderer rostra than those of *D. d. arizonae.*

Dipodomys deserti arizonae intergrade in a wide zone with *D. d. deserti* to the west in south central Arizona. Some specimens from the following localities in the zone of intergradation, when compared with typical *D. d. arizonae,* have slightly more ochraceous color and smaller cranial measurements: 16 mi W, 2 mi N Buckeye; 11 mi S, 7½ mi E Buckeye; Gila Bend, Maricopa County. One adult from 10 mi N Ajo, Pima County, has more of a pinkish buff color and some of its cranial characters are smaller.

Variations within the range of *D. d. arizonae* are not great. Specimens from the following localities show some degree of variation when compared to typical *D. d. arizonae*: Specimens from the vicinity of Scottsdale, Maricopa County, have more inflated mastoidal bullae and are larger in several skull measurements, especially in greatest length, basal length, and nasal length. Specimens from Phoenix, Maricopa County, and from Maricopa, Pinal County, have slightly more buffy color of the upper parts, paler arietiform markings, and paler ventral tail stripe. Adults from Gila Bend, from10 mi S Gila Bend, Maricopa County, and from 10 mi N Ajo, Pima County, are larger in total length and in maxillary breadth.

Recent field work by W. Goodpaster in central Arizona revealed an interesting transition in the habitat requirements of this subspecies of the desert kangaroo rat. The typical habitat of *D. deserti* is deep, loose, drifting sand or sand dunes. In his field notes, Goodpaster wrote that two specimens of *D. d. arizonae,* UI Nos. 27535 ♀ and 27536 ♀, from 6 mi N, 1 mi E Florence, were collected on 15 March 1963 in hard gravelly soil. This is the only locality known to me in which specimens of *D. deserti* were collected in gravelly soil. Although there is a possibility that the animals were foraging on the gravelly soil while their burrows are in the loose sandy soil, it is assumed, from Goodpaster's notes, that the animals were trapped near their burrows which were in the gravelly soil. This shift in the habitat requirement of the desert kangaroo rat is important from the evolutionary and distributional point of view of the species.

Specimens examined. A total of 133 specimens from:

ARIZONA. MARICOPA COUNTY: 9.7 mi N Dunlap [Ave.] and 7th St.,

and 0.3 mi W on Cave Creek Rd. [about 9.7 mi N Sunnyslope], 1 (UI); 5 mi N Shea Blvd. and Scottsdale Rd. [11 mi N Scottsdale], 1 (ASU); 15 mi N, 2 mi E of ASC [Arizona State College] at Tempe, 1 (ASU); 10 mi N, 2 mi E Scottsdale, 1,000 ft, 1 (ASU); 2.5 mi N Shea Blvd. on Scottsdale Rd. [8½ mi N Scottsdale], 1 (ASU); 8 mi N Scottsdale on Scottsdale Rd., 1 (UI); 1 mi W Scottsdale Rd., ¼ mi N Bell Rd., 1 (ASU), 1 (UI); 1 mi W Scottsdale Rd., 300 yds N Bell Rd., 1 (ASU); 250 yds W, 200 yds N Jct. Scottsdale and Bell Rds., 1 (ASU); 200 yds NW Jct. of Scottsdale and Bell Rds., 1 (ASU); 100 yds NE of Jct. Scottsdale and Bell Rds., 4 (ASU); 10 mi N Tempe to Bell Rd. on Scottsdale Rd., 1 (ASU); 5 mi N Scottsdale, 1 (ASU); 5 mi N, ½ mi E Scottsdale, 1,100 ft, 1 (ASU); Bell Rd. at Pima Rd., 1 (ASU); Phoenix, 1 (AMNH), 8 (USNM); 16 mi W, 2 mi N Buckeye, 1 (UI); 11 mi S, 7½ mi E Buckeye, 6 (UI); Gila Bend, 9 (USNM); 10 mi S Gila Bend, 3 (SDSNH). PINAL COUNTY: Florence Jct., 1 (AMNH); 6 mi N, 1 mi E Florence, 3 (UI); 5 mi N Florence, 1 (UI); 2 mi N Florence, 2 (MVZ); Sacaton, 1 (USNM); Maricopa, 5 (USNM); 1 mi E, 1 mi N Florence, 7 (UI); Florence, 4 (AMNH); 5 mi N Stanfield, 1 (UI); 11 mi W Casa Grande, 1 (KU), 11 (SDSNH); Casa Grande, 5 (USNM); 3 mi E Picacho, 6 (LACM); 3 mi SE Picacho, 17 (SDSNH); 4 mi S, 1 mi E Picacho, 17 (UI); Green's Reservoir, 1,600 ft, 2 (TCWC). PIMA COUNTY: 10 mi N Ajo, 1 (USNM).

Dipodomys deserti sonoriensis Goldman

Dipodomys deserti sonoriensis Goldman, Proc. Biol. Soc. Washington, 36:139, 1 May 1923, original description.

Type. Male, adult, skin and skull; No. 242306, U. S. Biological Surveys Collection; from La Libertad Ranch, 30 miles east of Sierra Seri, Sonora, México; obtained by Charles Sheldon, 3 January 1922, original number 22611–X.

Range. The coastal area of west central Sonora, México.

More specifically, from the southern banks of the Río de Magdalena, Sonora, south along the coastal region as far as the vicinity of Estero Testiota, and east along the Río de Sonora as far as the vicinity of Hermosillo. Limits of the range are not well known except the southern part. It is doubtful that this form of *D. deserti* will be found to occur much farther to the east beyond the coastal sand dunes, and beyond the vicinities of Hermosillo and Estero Testiota.

Diagnosis.

Size: Large; adult total length 349.0 to 364.4 mm; tail length in males 212.1 to 219.0 mm, and in females 201.0 to 221.5 mm; body length 147.0 to 154.4 mm.

Color: In general, Pale Ochraceous-Buff, purest on sides, heavily mixed with long blackish hairs on dorsum; arietiform markings blackish; orbital ring blackish; plantar stripe brownish with lighter shade on ventral side of toes; dorsal tail stripe blackish; ventral tail stripe dusky and usually present; subterminal band of tail blackish.

Skull: Large-sized; greatest length in males about 46.7 mm and in females 45.8 to 46.8 mm; maxillary arch weak, its posterolateral edge slightly flared; lacrimal large, its extension along posterior border of maxillary arch equaling about one-half of the distance to outer angle; interorbital breadth great, in males 14.5 to 14.8 mm and in females 14.2 to 15.2 mm; jugals slender, spur at its posterior end usually not well developed; mastoid bullae large, bullar depth 15.6 to 15.8 mm. Also see Table 11.

Comparisons. For comparisons with *Dipodomys deserti deserti* and *D. d. arizonae,* see accounts of those subspecies (pp. 85 and 94).

Remarks. Typical *Dipodomys deserti sonoriensis* is characterized by its large size, blackish color, thin maxillary arches, slender jugals, and inflated mastoidal bullae.

Goldman (1923:139) in his description of this subspecies stated that the size of the articulating area of the squamosal with the parietal, as viewed dorsally, is small. This area and the size of the squamosal, in general, are variable throughout the range of the species and do not provide reliable taxonomic characters.

Dipodomys deserti sonoriensis may intergrade with *D. d. deserti* to the north along the Río de Magdalena in northwestern Sonora. Lack of sufficient material from the northern part of the range of the former does not permit clear demonstration of this intergradation. Specimens from Cerro Prieto, however, are regarded here as intergrades. A subadult female from this locality has more of an ochraceous color, closer to that of *D. d. deserti.* Two other specimens from this locality lack the dark ventral tail stripe. Another variant is an adult male from Rancho Dolores with more reddish color than the rest of the series and the maxillary arches slightly more slanted posteriorly, similar to that of *D. d. deserti.* Several specimens from Bahía Kino are smaller in several skull measurements than is typical for *D. d. sonoriensis.*

The dark ventral tail stripe is not always present in specimens assigned to this race, but it has been present in 56% of the specimens examined. This ventral tail stripe is disrupted or broken in some specimens and continuous in others.

Three specimens from Estero Testiota were taken about 35 miles south of the southernmost recorded locality for this subspecies. The vicinities of Estero Testiota and Hermosillo most probably are the southern and southeastern limits, respectively, as no apparent suitable habitat is available farther south and southeast of them.

Specimens examined. A total of 77 specimens from:

SONORA. Cerro Prieto, 3 mi N Puerto de Lobos, 500± ft, 2 (MVZ); La Libertad Ranch, 30 mi E Sierra Seri, 1 (USNM); La Libertad Ranch, [30 mi E] Sierra Seri, 1 (USNM); Rancho Dolores, 7 mi ESE Rancho Libertad, 47 mi W Hermosillo, 300 ft, 8 (MVZ); 7 mi ENE Pozo Escalante, 2 (KU); 1 mi N Rancho de Costa Rica, Río Sonora, 270 ft, 4 (MVZ); Rancho Costa Rica, 45 mi SW Hermosillo, 15 (UCLA); Rancho de Costa Rica, Río Sonora, 200 ft, 1 (MVZ); Costa Rica Ranch, 1 (USNM); 15 mi W, 3 mi S Hermosillo, 7 (UI); 4 mi N Bahía Kino, 3 (LACM); 3 mi N Bahía Kino, 1 (LACM); Bahía Kino, 10 (SDSNH), 10 (UI); 1½ mi E Bahía Kino, 1 (LACM); 5 mi NE Estero Testiota, 7 (MVZ); Estero Testiota, 3 (MVZ).

Additional records. SONORA. Sand dunes, Puerto Libertad, 25 ft, 1 (UA, Cockrum and Bradshaw, 1963:8); vicinity of Hermosillo (Villa, 1941:371).

PHYLOGENY OF THE SPECIES *D. SPECTABILIS* AND *D. DESERTI*

Fossil history of the genus *Dipodomys* was reviewed by Setzer (1949) and Lidicker (1960). Members of this genus first appeared in the late Pliocene or early Pleistocene and evolved from the primitive heteromyid *Prodipodomys*. Different forms which belong to the genus *Prodipodomys* are known from the middle Pliocene to early Pleistocene (Hibbard, 1937, 1939, and 1962). *Prodipodomys rexroadensis* was described by Hibbard (1954:228) from the Upper Pliocene deposit of the Rexroad fauna, Meade County, Kansas. On the basis of the teeth only, Hibbard (1954:231) stated that this species can be considered as ancestral to *Dipodomys*. Gidley (1922:123) described *D. minor* from late Pliocene deposits from Benson, Arizona. If one follows Gazin (1942:486) in referring *Dipodomys minor* to the genus *Prodipodomys*, then the earliest member of the genus *Dipodomys* is *D. gidleyi* known from very late Pliocene or early Pleistocene deposits from Curtis Ranch, near Benson, Arizona. Setzer (1949:484) stated that *D. spectabilis* may have been the end product of the phyletic trend of *D. gidleyi* and that *Prodipodomys? minor* may have given rise to *D. ordii*. Thus, according to the available paleontological evidence, all modern species of *Dipodomys* were probably differentiated since late Pliocene or early Pleistocene.

As many as three centers of dispersal for the species of the genus *Dipodomys* have been proposed. Setzer (1949:498) proposed that southwestern Nevada and southeastern California, south to the northern deserts of México was a major center and that the low, hot, interior valleys and adjacent foothills of central California was a secondary center. Lidicker (1960:131) assumed that the high, dry, Mexican Central Plateau was a third minor center.

As stated by Mayr (1963:386), the original form of a species is usually found in the central part of the range of the species, while the

peripheral populations may deviate secondarily in different ways. Accordingly, it is assumed that the region of origin and the center of dispersal of *Dipodomys spectabilis* was in southwestern New Mexico and adjacent parts of Chihuahua. This is the northern part of the third minor center of origin of the genus which was proposed by Lidicker (1960). *D. spectabilis* probably originated in the middle Pleistocene. From its place of origin, the following three patterns of dispersal are assumed to have taken place. These patterns are partly based on the relationships among the different recognized subspecies and partly conjectural. One route was in a westward direction to south central Arizona and adjacent parts of Sonora, giving rise to *D. s. perblandus*. These populations are well differentiated and inhabit a somewhat different terrain from that of the parental stock (open desert vs. desert grassland). Later on, a southward invasion of these populations to west central Sonora resulted in the differentiation of *D. s. intermedius*. A second route of dispersal from the center of origin of the species was in an eastward direction to central New Mexico and from there southeastward to western Texas and northwestward to northwestern New Mexico and the adjacent area of northeastern Arizona. These populations comprise what is known now as *D. s. baileyi*. The third route was in a southeastward direction to south central Chihuahua giving rise to *D. s. zygomaticus*. From south central Chihuahua, the banner-tail invaded the lowlands of eastern Durango, and from there two routes were taken. A side route was taken in an eastward direction to west central Coahuila. From there it moved southeastward to southern Coahuila, northern Zacatecas, northern San Luis Potosí, and southern Nuevo Leon, and northwestward to northwestern Coahuila and southeastern Chihuahua. These populations inhabited a somewhat drier environment than that typical for *D. spectabilis*, and after isolation gave rise to *D. s. nelsoni*, a well-marked subspecies of *D. spectabilis*. The main route, from eastern Durango, continued in a southeastward direction to central Zacatecas, western San Luis Potosí, and eastern Aguascalientes where these populations gave rise, after being isolated, to *D. s. cratodon*.

Dipodomys deserti probably originated in early Pleistocene in the major center of origin of the genus, in southwestern United States, and most probably in southeastern California and the lower Colorado Desert. From the place of origin of this species, population dispersal probably took three main directions. The following patterns of dispersal of the populations are assumed, in part, from the relationships among the different recognized subspecies and, in part, from conjec-

ture. One population took a north northwestward route resulting in the differentiation of *D. d. aquilus* in northwestern Nevada. A second route was mainly in an eastward direction to south central Arizona, which gave rise to *D. d. arizonae*. A small population invaded the eastern banks of the Colorado River and moved northward, but did not reach the area now covered by Lake Mead. Populations on the eastern side of the Colorado River did not differentiate from the original population of southeastern California. The third route was mainly southeastward into northwestern Sonora and coastal areas of western Sonora, giving rise eventually to *D. d. sonoriensis* in west central Sonora. A small population invaded the northeastern coastal areas of Baja California. Populations in this region are still in direct contact with the parental populations in southeastern California and, although specimens from Baja California are slightly larger, they have not differentiated enough to become taxonomically distinct.

D. spectabilis occupies throughout its range several different types of habitats, whereas *D. deserti* occupies an almost uniform habitat, which suggests that the limits of tolerance of *D. spectabilis* are much greater than those of *D. deserti*. Although *D. spectabilis* is assumed to have originated later than *D. deserti*, the present geographic range of *spectabilis* is approximately twice that of *deserti*. This indicates that the rate of dispersal of *D. spectabilis* has been greater than that of *D. deserti*. *D. deserti* seems to occupy, at the present, almost all of the suitable habitat available to it, and, unless a change in its habitat requirements takes place or changes occur in the enivornment itself, the geographic range of this species will not change appreciably from its present condition. In contrast, some range extension is to be expected of *D. spectabilis*, especially in Sonora, Durango, Zacatecas, and San Luis Potosí due to the availability of some suitable habitat. The high degree of differentiation of most of the subspecies of *D. spectabilis*, in contrast with those of *D. deserti*, suggests that *D. spectabilis* has had a faster rate of evolution. Moreover, it seems that *D. deserti* is genetically more stable than *D. spectabilis*. This genetic instability of the latter species coupled with isolation and natural selection are believed to be important factors in its ability to adapt to different habitats and to give rise to more recognizable taxa than *D. deserti*.

In comparing the extent of the geographic variation in the morphology of the two species studied, it appears that this variation is more extensive in *D. spectabilis* than in *D. deserti*. It is postulated that this is partly due to the availability of more varied habitat and to a longer period of isolation of some of the populations of *D. spectabilis* in con-

trast with *D. deserti*. *D. spectabilis* gave rise in its evolutionary history to at least seven distinguishable living subspecies. These subspecies are at various levels of differentiation. Some are notably well differentiated and have nearly attained the specific level, as *D. s. nelsoni*, and to a slightly lesser degree as *D. s. perblandus*. Others are still less differentiated such as *D. s. baileyi*, *D. s. cratodon*, and *D. s. spectabilis*. The least differentiated is *D. s. zygomaticus*. Among the numerous factors responsible for the different degrees of divergence, the most important is the length of the period of geographic isolation. The zone of contact between *D. s. nelsoni* and *D. s. zygomaticus* is defined by a sharp shift in many character gradients and by a high degree of concordance in the characters studied which clearly indicate a secondary zone of intergradation. This zone most likely demonstrates that the contact between *D. s. nelsoni* and *D. s. zygomaticus* is relatively recent in the history of the species. *D. s. nelsoni* generally occupies an open desert type habitat which differs considerably from the range of the neighboring subspecies that occupy desert grassland. This difference in habitat probably further enhanced the differentiation of *D. s. nelsoni*. The high degree of divergence of this subspecies reflects a long period of isolation.

The zone of intergradation between *D. s. perblandus* and *D. s. spectabilis* also indicates secondary contact and strongly suggests a long period of isolation between these two subspecies. This zone is not so well defined as that between *D. s. nelsoni* and *D. s. zygomaticus*. The zone of contact between *D. s. perblandus* and *D. s. spectabilis* coincides closely with the presence of certain high ranges of mountains in southeastern Arizona—that is, the Empire, Santa Rita, and Patagonia mountains—which have been a highly effective barrier between the two subspecies. In general, *D. s. perblandus* occurs in low, open desert habitat, while *D. s. spectabilis* inhabits mixed desert grasslands at higher elevations. The different territory occupied by *D. s. perblandus* probably further enhanced its differentiation.

D. s. cratodon, which is presently isolated from the other subspecies, is not so well differentiated as either *D. s. nelsoni* or *D. s. perblandus*. It is likely that the geographic isolation of *D. s. cratodon* from its neighboring subspecies is more recent in the history of the species than that of either *D. s. nelsoni* or *D. s. perblandus*. Moreover, the habitat of *D. s. cratodon*, unlike that of the two aforementioned subspecies, does not differ appreciably from that of *D. s. zygomaticus* and *D. s. spectabilis*.

Dipodomys deserti consists of only four recognizable subspecies al-

though the species itself originated in early Pleistocene, according to some authorities. Furthermore, the level of differentiation of each of these subspecies is not so great as that found among most of the subspecies of *D. spectabilis*. This low level of differentiation is attributed to the fact that throughout its entire range *D. deserti* inhabits an almost uniform type of soil and encounters no effective geographic barriers that would permit isolation and differentiation. Also, *D. deserti* seems to have achieved a high degree of specialization for the type of habitat it occupies, which is reflected by its narrow limits of tolerance and by the presence of certain specializations in its morphology.

It is thought that the inflation of the mastoidal bullae and the elongation of the hind feet are indications of the specialization and adaptation in *D. spectabilis* and *D. deserti* for open habitat and desert life. Some investigators have postulated that bullar inflation is an adaptation for saltation. Hatt (1932) suggested that the inflated auditory and mastoid bullae may shift the skull's center of gravity backward and thus facilitate richochetal locomotion. Seton (1929) stated that the mastoid chambers contain some fluid and the mastoidal inflation is a specialization assisting in control of locomotion. Other investigators suspected that bullar inflation is an adaptation for acute hearing and this has been proved by Webster (1962) in his experiments with *D. merriami* and *D. spectabilis*. It may be postulated that the larger the bullae are, in relation to skull size, the better the animal is adapted to jumping and balancing and also the better equipped for an open habitat. Bullar inflation is believed to permit more acute hearing in the special atmospheric conditions that affect the sound-transmitting properties of air in hot climates. This in turn increases the ability of the kangaroo rat to detect and avoid predators while they are still some distance away. The elongation of the hind foot is an adaptation for the saltatorial mode of locomotion. Thus, the longer the hind feet are, in relation to the length of the body, the better the animal is adapted to this type of locomotion.

To determine the degree of specialization of each subspecies in relation to the other subspecies within the species, four indices are calculated. They are the bullar index, cranial index, pedal index, and index of total specialization. The bullar index shows the degree of bullar inflation in relation to the breadth across the maxillary arches. The cranial index shows the degree of mastoidal enlargement in relation to the greatest length of the skull. The pedal index shows the degree of hind foot elongation in relation to the length of the head and body. The index of total specialization shows the degree of specialization in

each subspecies in regard to the three aforementioned indices. The four indices are presented in Tables 12 and 13 for *D. spectabilis* and *D. deserti*, respectively. According to the index of total specialization, it appears that *D. s. nelsoni* is the most specialized and *D. s. intermedius* is the least specialized subspecies of the species *D. spectabilis* (Table 12). Also it appears that *D. d. deserti* is the most specialized and *D. d. sonoriensis* is the least specialized among the subspecies of *D. deserti* (Table 13).

Setzer (1949:564) concluded that "In general, the most primitive kinds of *D. ordii* occur at the periphery of the range of the species," and Lidicker (1960:206) stated that his study of *D. merriami* showed that "there is a definite tendency for the less specialized and presumably more primitive populations to inhabit the periphery of the range of the species." The present study on *D. spectabilis* and *D. deserti* does not show any uniform tendency in the peripheral forms to be less specialized in either of these two species. Also, this study shows that it is difficult to generalize that the peripheral or the central population is

TABLE 12
Indices of specialization in *Dipodomys spectabilis*

Subspecies in order of increasing total specialization	Bullar	Cranial	Pedal	Total
D. s. intermedius	1.096	.639	.354	69.6
D. s. perblandus	1.103	.639	.358	70.0
D. s. spectabilis	1.115	.639	.364	70.6
D. s. baileyi	1.119	.636	.365	70.6
D. s. zygomaticus	1.107	.643	.373	70.7
D. s. cratodon	1.102	.652	.372	70.8
D. s. nelsoni	1.185	.636	.368	72.9

TABLE 13
Indices of specialization in *Dipodomys deserti*

Subspecies in order of increasing total specialization	Bullar	Cranial	Pedal	Total
D. d. sonoriensis	1.268	.667	.362	76.56
D. d. arizonae	1.279	.668	.374	77.36
D. d. aquilus	1.285	.665	.378	77.60
D. d. deserti	1.280	.669	.382	77.74

the most specialized in a species. When a peripheral population becomes isolated during the process of dispersal, it may differentiate secondarily to a more specialized or to a more generalized form than the parental population. Among the several factors that may influence this secondary differentiation are the length of the period of isolation, the degree of difference in the genetic constitution, and the habitat differences.

Lidicker (1960) summarized the previous attempts to arrange the living species of the genus *Dipodomys* into a phylogenetic scheme and then presented his own. No such attempt has been made in the present study. But in order to determine how closely related *D. spectabilis* is to *D. deserti*, four indices were calculated for each species with use of the data presented in Tables 12 and 13 respectively. Also, the data from Setzer (1949:508) for *D. ordii* and from Lidicker (1960:207) for *D. merriami* were utilized and are presented in Table 14 along with those of *D. spectabilis* and *D. deserti*. From this table, three tentative conclusions can be drawn: (1) *D. spectabilis* is less specialized than *D. deserti* in all the indices studied; (2) *D. deserti*, besides being more specialized than *D. spectabilis*, is phylogentically far removed from it, contrary to what Lidicker (1960:134) had proposed; (3) *D. deserti* is the most specialized of the four species compared, and it is the most specialized species of the genus *Dipodomys*.

On the basis of total specialization (based on averages of six indices) and comparison of the visceral arrangement, Setzer (1949) regarded *D. deserti* as the most specialized species of the genus *Dipodomys* and retained it in a separate group from *D. spectabilis*. Lidicker (1960), considering all of the accumulated evidence together with his field experience, placed *D. deserti* in a separate subgroup within the Spectabilis Group. He suggested that it may, however, be desirable to re-

TABLE 14
Indices of specialization in four species of *Dipodomys*

Species in order of increasing total specialization	Bullar	Cranial	Pedal	Total
D. ordii (after Setzer, 1949)	—	.634	.370	—
D. spectabilis	1.118	.640	.364	70.74
D. merriami (after Lidicker, 1960)	1.155	.635	.377	72.20
D. deserti	1.278	.667	.374	77.32

tain *D. deserti* in a separate group following the Spectabilis Group. Burt's (1960) study of the bacular morphology showed that the baculum of *D. spectabilis* is very different from that of *D. deserti*. Most recently, in his study of the karyotypes of the genus *Dipodomys*, Stock (1974) also regarded *D. deserti* as the most specialized species of the genus. However, he placed it in a separate subgroup within the Heermanni Group. He also found differences in the diploid number and in the morphology of the chromosomes of *D. spectabilis* and *D. deserti*.

According to the indices arrived at in this study along with the available evidences which illustrate the differences between *D. spectabilis* and *D. deserti*, this latter species should be retained in a separate Deserti Group. Moreover, because of the high degree of specialization of *D. deserti*, the Deserti Group should be kept at the end of the phylogenetic scheme of the genus as it has been in earlier schemes.

SUMMARY

This study is based on the examination of 2,725 specimens from 689 localities of both *Dipodomys spectabilis* and *Dipodomys deserti;* 1,187 specimens from 368 localities for *D. spectabilis* and 1,538 specimens from 321 localities for *D. deserti.* Fourteen skull measurements and six external measurements were studied and the color of each specimen was analyzed.

The two species are characterized and notes are given about their habitat, longevity, predators, parasites, and molt. In each of the two species, the adults undergo one molt a year, usually in August for *D. spectabilis* and in July for *D. deserti.*

Notes on reproductive activities of both species are given. There is a slight difference in the length of the period of these activities and in the number of embryos per month between the northern and the southern populations in *D. spectabilis.* The period is longer and the number of embryos is larger in the southern populations. No such differences are found in *D. deserti.* The mean of the litter size in *D. deserti* is larger than that in *D. spectabilis.*

Color of the pelage in *D. spectabilis* is more stable than it is in *D. deserti.* The color in *deserti* seems to be correlated with the color of the soil.

The age of each specimen was determined primarily on the basis of tooth wear and the translucence of some of the skull bones. Five age-groups are recognized in *D. spectabilis*: juvenile, immature, subadult, young adult, and old adult, while in *D. deserti* four age-groups are recognized: juvenile, immature, subadult, and adult. No significant differences are found between the young adult and the old adult age-groups in *D. spectabilis.* In the statistical treatment and in the analysis of the infraspecific variation, only the adults are considered. Notes on dentition and the pattern of wear on the occlusal surface in each of the two species are given.

Variation within a population is analyzed and the coefficient of variation is calculated for each measurement studied for both species. No significant secondary sexual dimorphism is present in *D. spectabilis,* although noteworthy differences are found in nine measurements in *D. deserti.* Clinal variation is not clear from the measurements of *D. spectabilis,* whereas some of the measurements in *D. deserti* show some degree of clinal change in a north-south direction. Nasal length and rostral depth increase in size in this direction, and this is thought to be correlated with the temperature and humidity of the environment.

Geographic variation is more evident in *D. spectabilis* than in *D. deserti* although the latter is thought to have originated earlier. It is thought that this is due to the availability of more varied habitat and a longer period of isolation of some of the populations of *D. spectabilis* in contrast with *D. deserti.* The low degree of variability throughout the range of *D. deserti* is ascribed to the uniformity of the habitat, the absence of effective geographic barriers, and its narrow limits of tolerance.

Seven subspecies of *D. spectabilis* and four subspecies of *D. deserti* are recognized and formally diagnosed. *D. s. nelsoni,* formerly regarded as a full species, is herein regarded as a subspecies of *D. spectabilis; D. s. clarencei* is regarded as a consubspecific with *D. s. baileyi.*

Notes on the fossil history of the genus in general and of *D. spectabilis* and *D. deserti* in particular are given. It is assumed that *D. spectabilis* originated in the northern part of the Mexican Central Plateau and *D. deserti* in southeastern California. A pattern of dispersal for each of these two species is proposed.

Four indices are calculated for each subspecies of the two species and then for each species to determine their degree of specialization for acute hearing and for saltation. The data arrived at in this study do not show, in either of the two species, any uniform distribution of the less specialized or the more specialized subspecies within the range of each species. Within *D. spectabilis,* the most specialized subspecies is *D. s. nelsoni,* and the most generalized is *D. s. intermedius.* Within *D. deserti,* the most specialized subspecies is *D. d. deserti* and the most generalized is *D. d. sonoriensis.* Also, *D. deserti* is found to be more specialized than *D. spectabilis* and is the most specialized species in the genus *Dipodomys.* It is proposed here that *D. deserti* should be retained in its separate Deserti Group.

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