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Dipodomys spectabilis.

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Dipodomys spectabilis Merriam, 1890

Banner-tailed Kangaroo Rat

Dipodomys spectabilis Merriam, 1890:46. Type locality "Dos Cabezos, Cochise County, Arizona."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae. The species contains seven subspecies (Hall, 1981):

D. s. baileyi Goldman (1923:140). Type locality "40 miles west of Roswell, New Mexico."
D. s. clarencei Goldman (1933:467). Type locality "Blanco, San Juan County, New Mexico."
D. s. cratodon Merriam (1907:75). Type locality "Chicalote, Aguas Calientes, Mexico."
D. s. intermedius Nader (1965:50). Type locality "16.7 mi. SW Bámori, 1900± feet, Sonora, México."
D. s. perblandus Goldman (1933:466). Type locality "Calabasas, Santa Cruz County, Arizona (altitude about 3,500 feet)."
D. s. spectabilis Merriam (1890:46), see above.
D. s. zygomaticus Goldman (1923:140). Type locality "Parral, southern Chihuahua, Mexico."

DIAGNOSIS. The banner-tailed kangaroo rat (Fig. 1) is among the largest of the genus (Best, in press). The skull (Fig. 2) is large and heavy for *Dipodomys*, and the inflated mastoids are separated on top by about 3 mm, so that there is a distinct interparietal, cuneate in shape (Merriam, 1890). The only large species of *Dipodomys* with which *D. spectabilis* may be sympatric, or is likely to be confused, are *D. deserti* and *D. nelsoni*. All other species of *Dipodomys* that occur sympatrically, or that approach the range of *D. spectabilis*, can be distinguished by their smaller size.

The ranges of *D. spectabilis* and *D. deserti* approach each other in south-central Arizona; both have been collected at Florence, Pinal Co. (Hoffmeister and Nader, 1963) and within Organ Pipe Cactus National Monument, Pima Co. (Nader, 1978). In *D. deserti*, the mastoids meet immediately behind the parietals, having at most an inconspicuous spicule between them (Nader, 1978).

Dipodomys nelsoni differs from *D. spectabilis* in slightly smaller size, slightly paler color, much smaller skull (Dalquest, 1953), narrower maxillary region of skull, and shorter white tip of tail (Anderson, 1972). Within Chihuahua mean measurements (in mm) of *D. nelsoni*, *D. s. spectabilis*, and *D. s. zygomaticus*, respectively, are: total length, 308.1, 335.8, 335.6; length of tail, 180.1, 195.4, 193.7; length of hind foot, 46.8, 52.4, 51.4; length of ear, 14.9, 16.1, 16.4; and body mass (in g), 84.7, 119.7, 116.5 (Anderson, 1972). Though *D. nelsoni* and *D. spectabilis* may be sympatric, there is no reason to suppose that intergradation between them takes place (Anderson, 1972; Baker, 1956).

GENERAL CHARACTERS. Banner-tailed kangaroo rats are adapted morphologically for saltatorial locomotion (Howell, 1933). They have four toes on the hind foot and the hind legs and feet are larger and much longer than the forelegs. 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 black-tipped hairs, purest on the sides and lightest on the cheeks. The supraorbital and postauricular spots, hip stripes, forelimbs, 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 are grayish black to dusky and unite to form a continuous black or almost black band around the tail subterminally. The white lateral tail stripes gradually narrow beyond the proximal half of the tail and disappear at the subterminal band (Nader, 1978). Young are grayish, near avellaneous, on the back and only slightly brighter on the sides (Dalquest, 1953).

The skull is large, with inflated bullae (Fig. 2). The interparietal bone is variable in size and shape and is 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. A depression, 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. The external opening of the auditory meatus varies from round to oval in shape. The hyoid apparatus is composed of two parts, basihyal and a reduced thyrhyal. The basihyal is medium-sized with a prominent ventral ridge; the anteromedial border of the shoulders is somewhat round (Nader, 1978). The teeth are medium-sized to massive (Nader, 1966). The unworn P4 resembles that of *D. ordii*; that is, the transverse valley is narrow and deep, straight where it borders the protoloph, and nearly straight posteriorly (Dalquest and Carpenter, 1986). The upper incisors are grooved anteriorly and the lower incisors also may have a distinct shallow groove (Wood, 1935).

Mean measurements (in mm) of 296 adult males and 232 adult females from throughout the range of the species are: total length, 342.2 and 338.0, for males and females, respectively; length of body, 142.3, 142.0; length of tail, 199.2, 195.9; length of hind foot, 52.1, 51.8; length of ear, 15.8, 15.7; greatest length of cranium, 45.7, 45.2; maxillary arch spread, 26.5, 26.2; alveolar length, 6.3, 6.2; greatest depth of cranium, 15.3, 15.2; greatest width of cranium, 29.3, 29.0; mass, 126.3 g, 119.6 g (Best, in press). Measurements that vary the most geographically are total length, length of tail, and greatest length of skull; the least variable are alveolar length of the maxillary toothrow, least supraoccipital breadth, greatest breadth of the exoccipitals, and alveolar length of the mandibular toothrow. *Dipodomys s. spectabilis*, which occurs almost in the center of the range of the species, is intermediate in almost all measurements. The western populations, *D. s. perblandus* and *D. s. intermedius*, are smaller in most characters than *D. s. spectabilis*. However, *D. s. intermedius* is generally smaller than *D. s. perblandus*. Populations of *D. s. baileyi* in the northeastern part of the range have the largest measurements for most characters. The disjunct population of *D. s. cratodon* in the southernmost part of the range is similar in some characters to *D. s. spectabilis*. The northern populations usually are larger (Nader, 1978).

Dipodomys spectabilis is among the most sexually dimorphic

FIG. 1. A male *Dipodomys spectabilis baileyi* from 14.5 km N, 17.5 km E Monticello, Socorro Co., New Mexico (photograph by D. C. Keller).

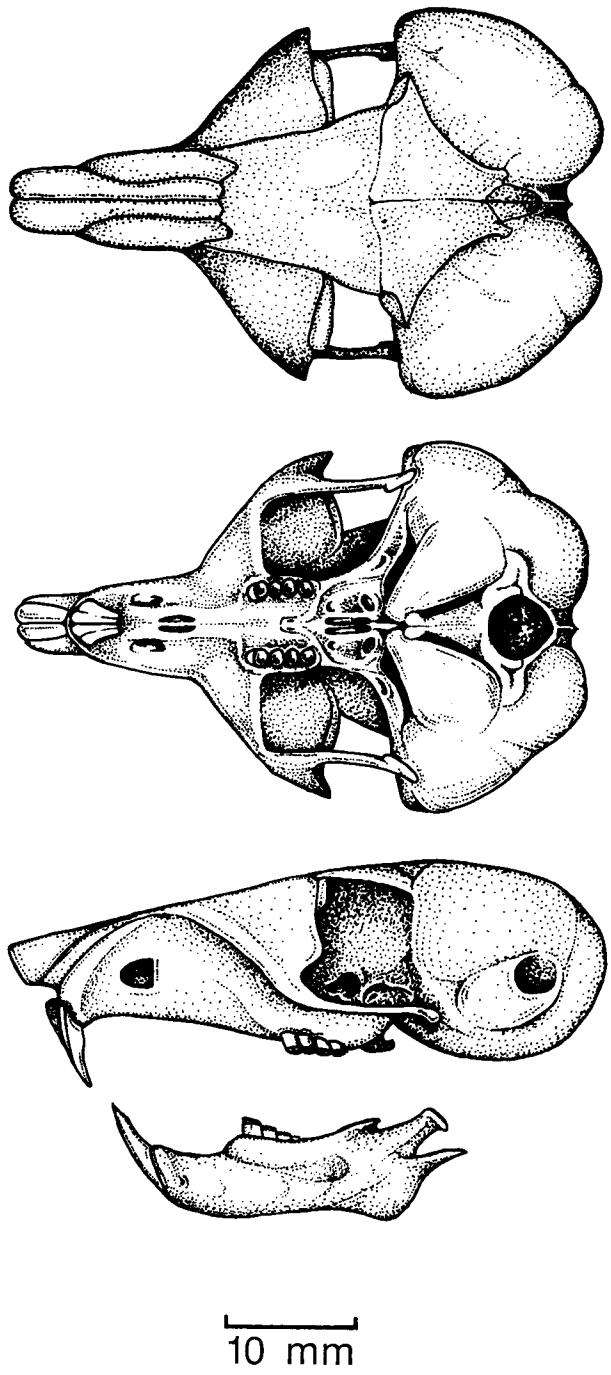

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Dipodomys spectabilis* (male, greatest length of cranium is 46.4 mm; Museum of Southwestern Biology 2738).

species of the genus. Males are significantly larger in several characters including total length, length of tail, greatest length of cranium, maxillary arch spread, greatest depth of cranium, and greatest width of cranium (Best, in press).

DISTRIBUTION. The banner-tailed kangaroo rat occurs from northeastern Arizona southward to Aguascalientes and San Luis Potosí, and from southern Arizona eastward to west Texas (Fig. 3). The range is continuous except for one disjunct subspecies, *D. s. cratodon*.

FOSSIL RECORD. Specimens several hundred years old were found in cave deposits near Cuatro Cienegas, Coahuila (Gilmore, 1947). Remains from Isleta Caves, Bernalillo Co., New Mexico, are of late Pleistocene-early Holocene age (Harris and Findley, 1964).

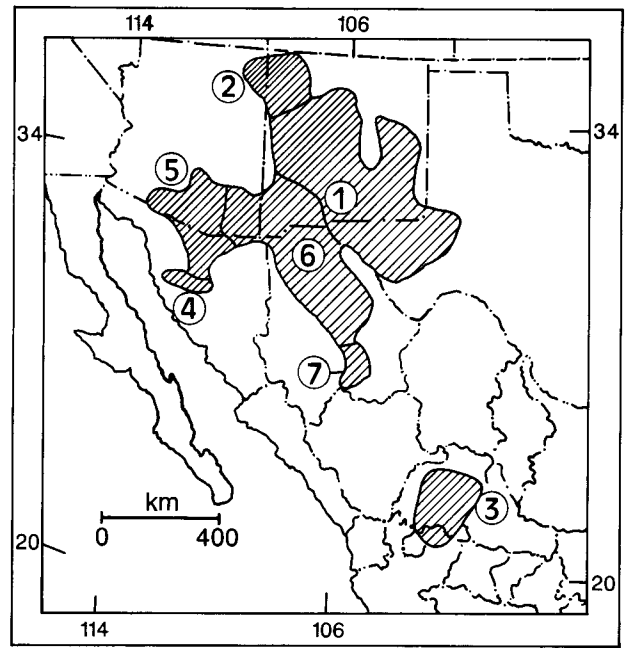

FIG. 3. Distribution of *Dipodomys spectabilis* in southwestern North America (Hall, 1981): 1, *D. s. baileyi*; 2, *D. s. clarencei*; 3, *D. s. cratodon*; 4, *D. s. intermedius*; 5, *D. s. perblandus*; 6, *D. s. spectabilis*; 7, *D. s. zygomaticus*.

Late Rancholabrean records include: Deadman Cave, Pima Co., Arizona (Mead et al., 1984); Dry Cave, Eddy Co., New Mexico; Howells Ridge Cave, Grant Co., New Mexico (Harris, 1977); U-Bar Cave, Hidalgo Co., New Mexico (Harris, 1985); and Fowlkes Cave, Culberson Co., Texas (Dalquest and Stangl, 1984). *D. gidleyi* possibly gave rise to *D. spectabilis* (Setzer, 1949; Wood, 1935). The fossil kangaroo rat, *Eodipodomys celtiservator*, is similar to *D. spectabilis* (Voorhies, 1975).

FORM AND FUNCTION. Color variation is not great (Nader, 1978). Mean length of hair is 15.3 mm (range = 14.5 to 16.0) and width ranges from 0.035 to 0.045 mm; long and relatively wide for the genus (Homan and Genoways, 1978). Subadult molt commences late in spring and ends early in winter with a peak in August. Adults molt once a year (mostly in August). 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 but disappears later. Then, a saddle-shaped area of new hair appears in the mid-dorsal 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, then posteriorly to the rump and hind limbs (Nader, 1978).

A skin gland is located in the mid-dorsal skin over the arch of the back (Quay, 1954), but is not visible in newborn young (Holdenried, 1957). In worn pelage, the gland may be visible without separating the hairs. The pelage of kangaroo rats kept in captivity without sand soon appears moist. When supplied with sand they return to their normal appearance. This condition is caused by excess oil that must be absorbed in a dust bath (Vorhies and Taylor, 1922). The mean tubule diameter of submandibular glands of *D. spectabilis* (58.5 μm) is larger than that of *D. merriami* (50.9 μm; Mitchell, 1970).

The baculum (Fig. 4) is the largest in the genus (Best and Schnell, 1974; Burt, 1960). The bulbous basal end is sculptured in old animals, and is higher than wide. From the basal end the shaft tapers gradually to the pointed tip, upturned at approximately a right angle to the nearly straight shaft (Burt, 1960). Bacula average (in mm) 16.7 long, 2.3 wide at the base, and 2.6 high at the base (Best and Schnell, 1974).

The auditory system of *D. spectabilis* is highly specialized (Babighian et al., 1975; Beecher, 1969; Bledsoe and Moushegian, 1980; Caspary, 1972; Caspary et al., 1977; Crow et al., 1978; Moushegian and Rupert, 1970*a*, 1970*b*; Moushegian et al., 1975; Rupert and Moushegian, 1970; Stack and Webster, 1971*a*, 1971*b*; Stillman, 1972; Webster, 1962; Webster and Webster, 1980). For example, the outstanding morphologic feature of the middle ear is

the extreme hypertrophy of the middle-ear cavity. The middle ear lacks superior and lateral ligaments of the malleus. The ossicles are suspended by the anterior ligament of the malleus and posterior ligament of the incus that form the axis of rotation. The transformer ratio of the tympano-ossicular system is 97.2:1. There are 4.25 turns to the cochlear duct (Webster, 1961). The middle ear volume is 1.00 cm^3, the relative middle ear volume is 0.28 cm^3, the tympanic membrane diameter is 6.34 mm, the length and width of the stapes footplate are 1.65 and 0.87 mm, respectively, and the lever arms are 3.61 mm for the malleus and 1.08 mm for the incus (Webster and Webster, 1975). Contrary to physiological and behavioral evidence that suggests they should not be able to localize low-frequency sounds, *D. spectabilis* demonstrates escape behavior based on the location of the sound source (McClelland and Schlafman, 1975).

Banner-tailed kangaroo rats have an apparent lack of specific angiotensin II binding sites in the brain (Harding et al., 1981), and the large perikarya in the accessory olfactory bulbs are arranged in loose bands as in most other mammals (Switzer and Johnson, 1977). Based on brain anatomy, *D. spectabilis* may have abilities that lie somewhere between *D. ordii* and *D. merriami* (Dressler, 1979).

Adaptation of the banner-tailed kangaroo rat to environments requiring conservation of body water is correlated with larger numbers of supraoptic nuclei cells with multiple nucleoli (Hatton et al., 1972). *D. spectabilis* has numerous other adaptations for survival in arid environments (Schmidt-Nielsen and Schmidt-Nielsen, 1952); for example, the highly concentrated urine is alkaline, which indicates *D. spectabilis* consumes a considerable amount of succulent food (Schmidt-Nielsen et al., 1948). The glomerular filtration rate is 0.68 ml min^{-1} 100 g body $mass^{-1}$ (range = 0.17 to 2.22; Schmidt-Nielsen, 1952). *D. spectabilis* shows a delay in the excretion of water and saline; only potassium chloride is excreted promptly (Cole et al., 1963). The ratio of evaporation to oxygen consumption does not change when activity is increased (Raab and Schmidt-Nielsen, 1971). During food deprivation polydipsia occurs, and in water-deprived animals there are only slight elevations in plasma (Wright and Harding, 1980). Nicotine causes a delay in the onset of diuresis and an increase in urine osmolality and chloride concentration when water is readily available, and it causes induced antidiuresis in water-deprived animals (Randle and Haines, 1976). *D. spectabilis* exhibits greater plasma-arginine-vasopressin at baseline and during prolonged dehydration than rats (*Rattus*; Stallone and Braun, 1981).

If banner-tailed kangaroo rats breathe air with low moisture content outside of burrows, the rate of evaporation from the lungs could exceed the rate of formation of metabolic water. The higher humidity in burrows is necessary for water balance. Formation of metabolic water, when the animals breathe the fairly moist air in burrows, leads to an ultimate gain in water (Schmidt-Nielsen and Schmidt-Nielsen, 1950*a*).

The rate of oxygen consumption is 1.40 ml g^{-1} h^{-1} and pulmocutaneous water loss is 0.57 mg H_2O/ml O_2 (Schmidt-Nielsen and Schmidt-Nielsen, 1950*b*). Oxygen consumption decreases in response to a combination of elevated carbon dioxide and water vapor pressure, relative to elevated carbon dioxide in dry air (Kay, 1977). A model to predict respiratory water loss from terrestrial vertebrates was evaluated based upon data for *D. spectabilis* (Welch and Tracy, 1977). A steady-state model of the heat and water transfer occurring in the upper respiratory tract of *D. spectabilis* illustrated the importance of nasal passage geometry in enhancing the recovery of water from air expired. In addition, the absence of a highly-vascularized lining in the entry region of the nasal passages may affect temperature distribution in the nose-tip region (Collins et al., 1971).

Mean body temperature of banner-tailed kangaroo rats acclimated to 25°C is constant at ambient temperatures from −5 to 15°C, and is reduced in the thermoneutral zone (20 to 30°C). The lethal air temperature is 40°C, and there is no response of body temperature to levels of carbon dioxide normally found in the burrow environment. There may be a decrease in body temperature with lower vapor density or high saturation deficit, but the major factor affecting body temperature is ambient temperature (Kay, 1975). Average hematocrit is 45.7 (*SD* = 5.4; range = 40 to 50; Neal and Wood, 1965). Respiratory characteristics of *D. spectabilis* blood are similar to those of the blood of white rats (*Rattus*; Gjönnes and Schmidt-Nielsen, 1952).

ONTOGENY AND REPRODUCTION. *Dipodomys spectabilis* reproduces year-round, except perhaps in October and November. Onset and termination are earlier in northern populations that include *D. s. perblandus*, *D. s. intermedius*, and *D. s. spectabilis*, than in southern populations that include *D. s. zygomaticus* and *D. s. cratodon*. In northern populations, the earliest pregnancy was 10 January and the latest 8 September; in southern populations, the earliest was 1 December, the latest 26 August. The largest number of pregnancies in northern populations is in April, and in the south largest numbers are in December, June, and July (Nader, 1978).

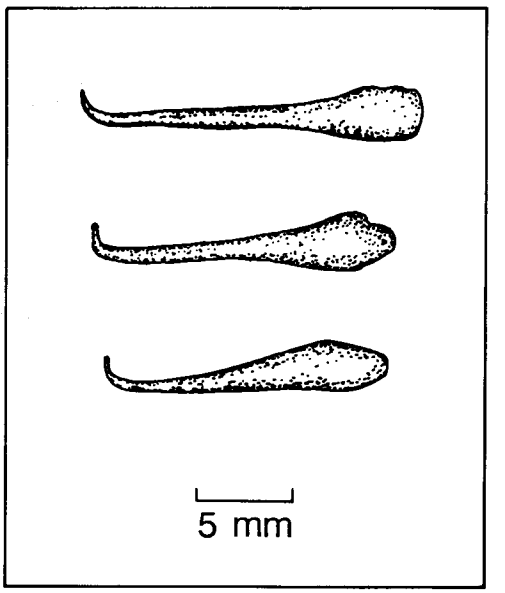

FIG. 4. Lateral views of representative bacula of (from top to bottom) *Dipodomys spectabilis baileyi* from New Mexico, *D. s. zygomaticus* from Chihuahua, and *D. s. cratodon* from Zacatecas.

After copulation the vagina becomes plugged with a translucent material with a consistency of stiff gelatine. This probably occurs soon after coitus, because individuals taken in this condition have no embryos (Vorhies and Taylor, 1922). The gestation period is 22 to 27 days (Bailey, 1931).

There are one to three litters/year (Holdenried, 1957; Vorhies and Taylor, 1922). One female delivered a second litter 42 to 49 days after her first, and a third litter 37 to 42 days after the second; in both instances she was lactating at conception (Holdenried, 1957). The largest embryo recorded had a crown–rump length of 60 mm (Nader, 1978). Neonate mass is 7.8 g and litter mass is 18.7 g (Jones, 1985). At birth the young are toothless, hairless, wrinkled, the eyes and ears are closed, and they show the color pattern of adults in shades of pink. At 14 days their eyes open and at 25 days they first fill their cheek pouches. They are weaned at 20 to 25 days of age (Bailey, 1931).

The size (in mm) of two 2-week-old young was: total length, 90, 93; length of tail, 38, 38; length of hind foot, 24, 24; mass, 13.3 g, 12.6 g. These young had fine velvety fur with tails nearly naked, the body was the color of the dark underfur of the adult, and the white markings of the adult were pinkish-white (Vorhies and Taylor, 1922). Young males grow faster in terms of mass than young females (Holdenried, 1957); age at maturity is 300 days (Jones, 1985).

Deciduous incisors are the first teeth to erupt from the alveolar ridge and are lost shortly thereafter. M1 and deciduous PM4 erupt shortly after the incisors, probably at 13 or 14 days of age, and persist for a short period before being lost. Both deciduous PM4 and M1 show some wear before eruption of M2. M2 shows some wear before eruption of M3 that 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 jaw follows the same general pattern as that of the upper jaw, except permanent incisors and M3 are slower in eruption and development (Nader, 1978).

ECOLOGY. Banner-tailed kangaroo rats live in desert grasslands with scattered shrubs (Fig. 5*A*, *B*; Monson, 1943; Vorhies and Taylor, 1922). Near Tucson, Arizona, they are more common among

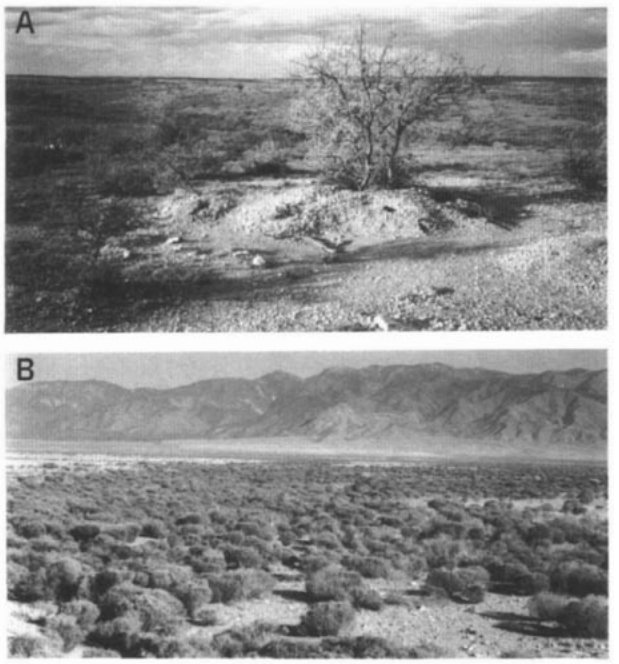

FIG. 5. (A) A mound constructed by *D. s. zygomaticus* 18.4 km ENE Hidalgo del Parral, Chihuahua (photograph by C. Intress) and (B) habitat of *Dipodomys spectabilis baileyi* 13 km SE Belen, Valencia Co., New Mexico (photograph by T. E. Garrison).

Acacia, *Mimosa*, and *Prosopis*. The presence of a luxuriant grass flora probably is a factor in the greater abundance of *D. spectabilis* (Vorhies and Taylor, 1922). They are at the base of alluvial fans in the Huachuca Mountains, Arizona, and from there farther out into the desert. They are more common in open grassland with fewer mesquites than *D. ordii* and *D. merriami* (Hoffmeister and Goodpaster, 1954). In eastern New Mexico, they occur in a mixed-grassland climax dominated by *Bouteloua gracilis*, *Yucca*, *Prosopis juliflora*, *Opuntia imbricata*, *Aristida*, *Cenchrus*, *Panicum obtusum*, *Gutierrezia*, *Salsola kali*, and mixed small annuals (Best, 1972), and in central New Mexico, they are found in vegetation including *Sporobolus*, *Aristida*, *Muhlenburgia*, *Tridens*, *Bouteloua*, *Andropogon*, *Mentzilia pumila*, and *Gutierrezia sarothrae*, with *Salsola kali* and *Yucca glauca* sparsely intermixed (Schroder and Geluso, 1975). In western Texas, their distribution is related to the presence of *Larrea divaricata* and hard-pan soils (Packard and Judd, 1968) and to loose sand and sandy-loam blown into dunes where the vegetation is *Quercus havardi* (Archer, 1975). In Mexico, banner-tailed kangaroo rats occur in the Sonora and Chihuahua-Zacatecas biotic provinces (Goldman and Moore, 1946). In northern Sonora, they live in habitat dominated by *Prosopis* under which there is grass, mostly *Aristida* and *Bouteloua* (Dice and Blossom, 1937). In San Luis Potosí, they are only on the open, flat desert where the soil is deep and sandy (Dalquest, 1953). Other soils occupied by *D. spectabilis* include: firm, gravelly, or rocky soil (Santa Rita Mountains, Arizona); loamy soil (Gunsight, Arizona); stony mesas (Carlsbad and Pecos Valley, New Mexico); and hard-limy ridges (Monahans, Texas; Vorhies and Taylor, 1922).

Dens ordinarily are constructed in open locations, but many are built under protection of shrubs (Monson and Kessler, 1940). *D. spectabilis* may build mounds on earthen structures such as dams of stockponds. However, they do not build dens on sites subject to flooding (Compton and Hedges, 1943). Soil from dens contains more soluble salts than adjacent areas. These increases are pronounced for calcium, magnesium, bicarbonates, and nitrates (Greene and Reynard, 1932). Burrows also are characterized by increased values for moisture-equivalent and water-holding capacity of the surface soil and by a larger percentage of finer-sized soil particles (Greene and Murphy, 1932). Banner-tailed kangaroo rat mounds have more annual plants on them than surrounding areas; however, total plant cover generally is less on mounds (Moroka et al., 1982).

In territory occupied by *D. spectabilis*, burrows are conspicuous (Fig. 5A). These low, rounded mounds rise to varying heights above the surface of the surrounding soil; the height depends upon the soil and location of the mound. Mounds are in centers of cleared areas as large as 10 m in diameter. There are three to 12 openings in each mound. Radiating in various directions from some of the openings are well-used runways, some extending 30 to 50 m or more to neighboring burrows. Usually one or more smaller burrows are found near the mound (Vorhies and Taylor, 1922).

Mounds are nearly circular averaging 4.1 m at their widest dimension (range = 2.9 to 5.1) and 4.0 m for their narrowest (range = 2.6 to 5.0). The average height above the surrounding level ground is 30.5 cm (range = 20 to 41; Reichman et al., 1985). Dimensions of mounds vary geographically (Best et al., 1988). The mound is constructed by cleaning out chaff and other food refuse, and through repair and modification of tunnels. Ejected material is thrown out fan-wise from openings. The entrances are 10 to 15 cm in diameter and situated above the surface of surrounding soil. Some tunnels form chambers and some have stored material (Vorhies and Taylor, 1922). Mounds average 10 caches each (range = 6 to 20). Most caches occur near 30 cm in depth or below 50 cm. Most caches are approximately one-third of the distance from the mound center to the edge and are on the north or northwest side of mounds (Reichman et al., 1985). The major portion of the tunnel system is within 50 cm of the surface, but usually one branch goes deeper, and this is likely to be the one containing the nest. Tunnels average about 8 cm in height and 11 cm in width, though there is considerable variation. Portions used for storage are 15 to 25 cm in diameter. The nest cavity is 17 to 23 cm in diameter and is composed of finer, softer, and more chaffy material than the storage areas. There are no special pockets for deposit of feces because such may be found throughout the den and is mixed with food refuse that practically carpets the entire tunnel system. The two to four subsidiary burrows are simple and contain no storage. They are shallow (up to 48 cm) and appear to be places of refuge (Vorhies and Taylor, 1922).

One new mound appeared in 3 years among 287 existing mounds, and six new mounds appeared in 2 years at a site containing 105 mounds (Jones, 1984). New mound construction requires at least several months (Best, 1972; Jones, 1984). Each new mound begins as a small satellite burrow near an existing mound. These are enlarged into small raised mounds in a minimum of 2 months, then into full size mounds in at least another 2 months (Jones, 1984). Mounds that are not maintained constantly soon collapse (Best, 1972; Jones, 1984; Vorhies and Taylor, 1922).

Though mounds may appear to be in use, kangaroo rats may not be present at all of them (Monson and Kessler, 1940); 39 to 95% are occupied (Jones, 1984). In central New Mexico, there were 2.6 mounds/ha, and only 79 of 121 mounds were active. The density of active mounds was 1.7/ha. The mean distance between occupied mounds was 43.7 m and between all mounds 36.3 m. All mounds showed a uniform spatial distribution, whether occupied or not. Mound distribution may indicate that *D. spectabilis* minimizes intraspecific interactions by spatial means (Schroder and Geluso, 1975).

About 0.5 m within an open-mouth burrow the daily range in temperature is less than 5°C, though the mean maximum temperature of the soil surface may reach 65°C. Deep in the burrow the temperature is nearly static at about 27°C. A similar relationship between soil-surface, air, entrance-tunnel, and deep-burrow temperatures exists throughout the year (Vorhies, 1945). Burrow humidity generally is near saturation and is related to burrow temperature and surface humidity. Carbon-dioxide concentration is always higher than outside the burrow. Surface-wind velocity probably plays a role in burrow ventilation (Kay and Whitford, 1978).

In southeastern Arizona food is stored in spring and autumn. Some stored material may be found at any time of the year in any mound; the largest quantity usually in autumn and winter and the smallest in July or August. On the Santa Rita Range Reserve, Arizona, the stored material weighed from 5 to 4,127 g/mound. Stored food may be segregated by plant species, though stores of any one kind may be found in several places through the mound; often the material is mixed. The most common foods are *Bouteloua* and *Aristida* in southeastern Arizona and *Sporobolus cryptandrus* near Albuquerque, New Mexico. At times green and succulent portions of plants are eaten (Vorhies and Taylor, 1922). The 13 species of plants recovered from burrows in Texas showed differences among localities (Ramsey and Carley, 1970). Addition of seeds to study plots in the western Chihuahuan desert caused a threefold increase

in numbers of *D. spectabilis* and a slight decrease in numbers of smaller species (Munger et al., 1983).

Banner-tailed kangaroo rats climb in *Ephedra* to harvest the flowers (Reichman, 1983). The predominant food is *Bouteloua rothrockii* in southern Arizona (Monson, 1943). In southern New Mexico, they ate 64.6 kg km^{2-1} $year^{-1}$; that is, 42% green vegetation, 11% succulent vegetation (largely *Opuntia* pods and *Yucca* flowers and culms), 37% seeds, 4% Lepidoptera larvae, and 6% rodents. In 21 dens, there was an average of 1 kg/den of stored food representing 21 species of plants. Of these plants, 18% were perennial grasses, 23% annual grasses, 43% snakeweed (*Gutierrezia*), and 7% peppergrass (*Lepidium*; Wood, 1969). In 21 excavated dens, 1,018 kg of stored food was found per km^2. In western Texas, their cheek pouches contained dried feces presumably used as food (Miller, 1939). In San Luis Potosí, kangaroo rats had cheek pouches bulging with dry, green grass. Those of some individuals were so crammed with grass that the material removed from the pouches of an individual filled two cupped hands (Dalquest, 1953).

Banner-tailed kangaroo rats select sugar solution over water (Wagner, 1968*a*, 1968*b*). They also select slightly moldy seeds over moldy seeds, dry seeds, and unmoldy, imbibed seeds, apparently taking advantage of beneficial effects of molds but avoiding the liabilities (Reichman and Rebar, 1985). *Dipodomys spectabilis* actively moves seeds within its burrows to increase mold growth on sterile seeds and inhibit further growth on sufficiently moldy seeds (Reichman et al., 1986). There are no obvious temporal relationships between use of seeds and when they are gathered. Seeds stored early and late in a 4-month study period were significantly depleted after the 4 months, whereas those stored during the middle of the experimental period, when native seeds were abundant, were not depleted. Mycologic analyses of caches revealed at least 23 species of fungi. Fungal colonists are more abundant and diverse in caches made in the middle of the caching period than early or late in the period (Reichman et al., 1985).

Invertebrates, other than parasites, associated with *D. spectabilis* include grasshoppers (Orthoptera), wingless locusts (*Ceuthophilus*; Vorhies and Taylor, 1922), cave crickets (*Ceuthopilus lamellipes*), cockroaches (*Arenevaga erratica*), scorpions (*Centrurus* and *Vejovis sinigerus*), black widow spiders (*Latrodectus mactans*), centipedes, and other insects and spiders (Monson, 1943). Amphibians include toads (Monson and Kessler, 1940), and reptiles include rattlesnakes (*Crotalus*; Vorhies and Taylor, 1922), bullsnakes (*Pituophis*), kingsnakes (*Lampropeltis getulus*; Monson, 1943), geckos (*Coleonyx variegatus*), and other lizards (Vorhies and Taylor, 1922).

Banner-tailed kangaroo rats are sympatric with five other species of heteromyids in southern Arizona, *Perognathus flavus, P. amplus, Chaetodipus baileyi, C. penicillatus*, and *D. merriami* (Wondolleck, 1978). Additional mammals associated with these kangaroo rats include *Spermophilus tereticaudus, Ammospermophilus harrisii* (Vorhies and Taylor, 1922), *Sylvilagus auduboni, Onychomys leucogaster* (Holdenried, 1957), *Neotoma albigula, Peromyscus maniculatus, P. eremicus* (Gibbs, 1955), *Spermophilus spilosoma, Geomys bursarius, Chaetodipus hispidus, D. ordii, Reithrodontomys, Peromyscus leucopus, Sigmodon hispidus, Neotoma micropus, Mus musculus, Lepus californicus, Canis latrans, Vulpes, Taxidea taxus, Mustela frenata*, and *Antilocapra americana* (Best, 1972). Occasionally, banner-tailed kangaroo rats may live in old *Cynomys* or *D. ordii* burrows (Vorhies and Taylor, 1922). *Neotoma micropus* may coexist in the same mound with *D. spectabilis* where absence of suitable den materials or sites causes *Neotoma* to encroach upon the mounds; the results seems to be rather atypical mounds (Ramsey and Carley, 1970). Seed distribution does not play a role in the coexistence of *D. spectabilis* with *D. merriami* (Frye and Rosenzweig, 1980).

Several species prey on *D. spectabilis*, including badgers (*Taxidea taxus*), kit foxes (*Vulpes macrotis*; Nader, 1978), bobcats (*Lynx rufus*), coyotes, (*Canis latrans*), great horned owls (*Bubo virginianus*), and barn owls (*Tyto alba*; Vorhies and Taylor, 1922). Like other *Dipodomys*, banner-tailed kangaroo rats are eaten by humans in parts of San Luis Potosí. Individuals are killed at night with sticks, but apparently no attempt is made to dig them from their burrows (Dalquest, 1953). They are highly palatable to man (Gilmore, 1947).

Banner-tailed kangaroo rats are resistant to plague infection (*Pasteurella pestis*; Holdenried and Quan, 1956). Two protozoan parasites, *Eimeria scholtysecki* and *E. balphae*, have been found (Stout and Duszynski, 1983), and a cestode, *Catenotaenia linsdalei*, was recovered (Guay and Senger, 1962). Ticks and mites include *Dermacentor parumapertus, Ischyropoda armatus, Haemolaelaps glasgowi, Eubrachylaelaps crowei* (Eads et al., 1952), *Trombicula* (Vorhies and Taylor, 1922), *Hirstionyssus incomptus* (Strandtmann and Morlan, 1953), and *Listrophorus* (=*Geomylichus*) *dipodomius* (Radford, 1953).

Fleas found on *D. spectabilis* include *Meringis arachis, Anomiopsyllus hiemalis* (Eads, 1950), and *Ctenophthalmus* (Vorhies and Taylor, 1922). In Santa Fe Co., New Mexico, the following fleas were reported from 1,128 banner-tailed kangaroo rats: *Hoplopsyllus affinis, Meringis jamesoni, M. nidi, M. parkeri, M. rectus, Rhadinopsylla multidenticulatus, Monopsyllus exilis, Orchopeas sexdentatus, Thrassis campestris*, and *T. pansus* (Morlan, 1955). Of the 1,128 kangaroo rats, 792 were infested with 6,244 *Meringis rectus* and 462 with 3,184 *M. nidi* (Holdenried and Morlan, 1956). There were 12,361 fleas on 771 *D. spectabilis* in Chaves Co., New Mexico (Rail et al., 1969). They were: *Meringis rectus* (87% of the fleas), *M. nida, M. bilsingi, Thrassis fotus, T. aridis, Hoplopsyllus glacialis, Anomiopsyllus novomexicanensis, Rhadinopsylla fraterna, Echidnophaga gallinacea, Polygenus gwyni, Megarthroglossus bisetis*, and *Pulex irritans*. Other fleas on banner-tailed kangaroo rats from that area are *Meringis dipodomys, Rhadinopsylla multidenticulata, Euhoplopsyllus glacialis*, and *Pulex simulans* (Graves et al., 1974). Chlorphoxim is an effective oral systematic insecticide for control of fleas on *D. spectabilis* (Miller et al., 1977).

BEHAVIOR. Banner-tailed kangaroo rats are active all year, they are nocturnal, they do not hibernate or estivate, and when weather is rainy, wet, or cold, they remain in their burrows (Vorhies and Taylor, 1922). Maximum activity is about 20 min after sunset, thereafter declining throughout the night (Lockard and Owings, 1974*a*). No seasonal differences are evident in activity patterns, and the average animal is away from its burrow 43% of the night in spring, 47% in summer, and 39% in autumn. Adults spend 58% of the night hours inside or on the mound and less than 22% of their time more than 6 m from their burrows, but they average 68 m/foraging trip and total 350 m/night of foraging travels. Home ranges, calculated by three methods, average from 412 to 717 m^2 and activities are confined to small areas near mounds (Schroder, 1979), usually within about 160 m (Holdenried, 1957).

Activity is about 3 times greater when the moon is down than when it is up, and shifts somewhat from the open to vegetation cover when the moon is up (Lockard and Owings, 1974*a*). Seasonal variation in moonlight-avoidance possibly is related to caching (Lockard and Owings, 1974*b*). An artificial moon in the natural habitat also inhibits activity (Lockard, 1975). The activity pattern is nocturnal from November through March, with an early-evening peak and less activity during moon-up than moon-down. However, during a drought moonlight-avoidance ceased and nocturnal activity increased, including a small amount of daylight activity. Daylight activity increased during summer, becoming equal to night activity, then began to return to the usual nocturnal pattern at the same time as new vegetation appeared in response to summer rain (Lockard, 1978). However, some evidence indicates moonlight does not affect activity (Schroder, 1979).

Banner-tailed kangaroo rats have good swimming ability and stay drier and float higher than other small rodents, possibly because of the oily secretion on the pelage from the dorsal oil gland (Stock, 1972). Both sexes are strongly attracted to sandbathing sites previously used by conspecifics (Laine and Griswold, 1976). Scents left during sandbathing apparently do not communicate information on reproductive status, but *D. spectabilis* sandbathes to scent-mark its territory and may use scents to distinguish familiar neighbors from unfamiliar conspecifics (Randall, 1987*b*).

Sounds made by *D. spectabilis* include a high-pitched "peeee" lasting about a second (Gibbs, 1955), growls (Hoffmeister and Goodpaster, 1954), squeaks (Bailey, 1931), squeals and chuckles (Vorhies and Taylor, 1922), and drumming (Bailey, 1905; Randall, 1984). If a scratching or tapping sound is made at the mouth of a burrow, even in the daytime, one is likely to hear a muffled tapping in response (Vorhies and Taylor, 1922). These kangaroo rats advertise their territories by footdrumming and use it as a long-distance warning signal; chasing is used as a closer-distance threat. They footdrum on or near their mounds at night in response to footdrums of neighbors and during mound challenges. There are no sexual differences in

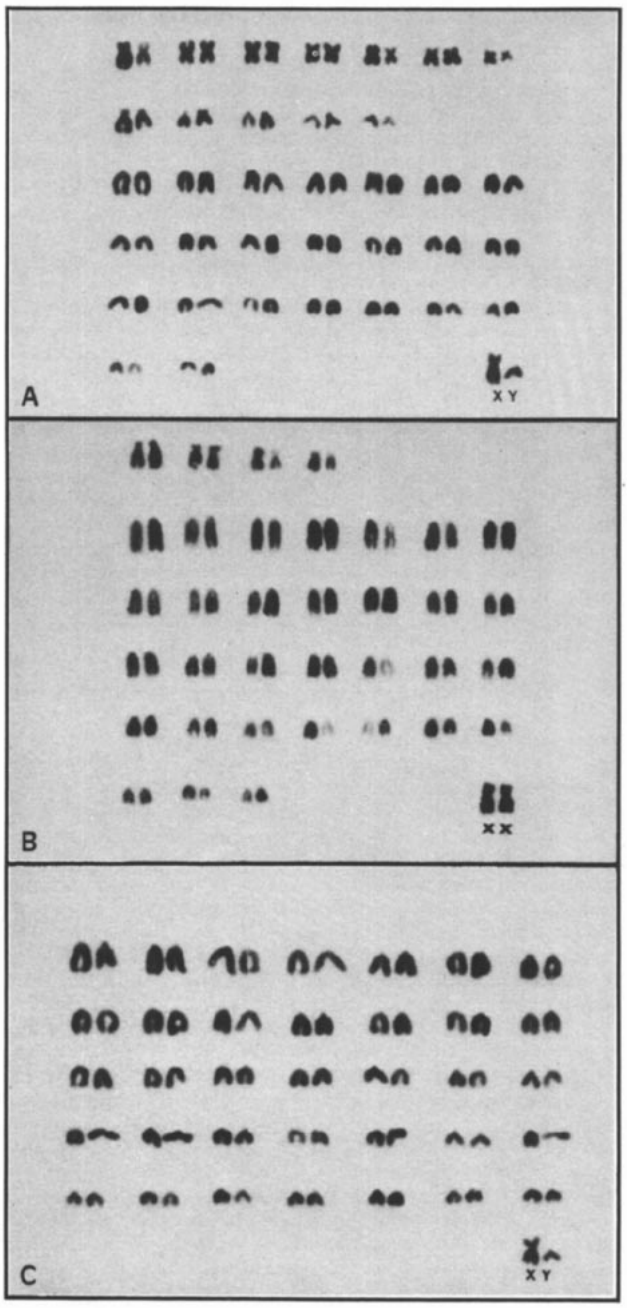

FIG. 6. Representative karyotypes of (A) *Dipodomys spectabilis baileyi*, (B) *D. s. perblandus*, and (C) *D. s. spectabilis* (from Hsu and Benirschke, 1975).

footdrumming, and juveniles frequently perform the behavior. They can differentiate between the footdrums of neighbors and strangers. Adults increase footdrumming rates at high population densities, but juveniles footdrum at high rates regardless of the population size (Randall, 1984). They footdrum at long ranges to repel potential intruders and also at close ranges when territories are threatened by persistent intruders (Ward and Randall, 1987). Footdrumming is also used as an anti-predator response toward snakes, accompanied by alert postures, jumping back, kicking sand, and avoidance. *D. spectabilis* does not footdrum in response to aerial predators (Randall and Stevens, 1987).

Although three or four individuals occasionally may be trapped at a mound, more than two are seldom caught. Usually only one animal occupies a mound, except when young are present (Jones, 1984; Vorhies and Taylor, 1922). Most adult females primarily use one mound, but often include adjacent mounds within their home range. Of 139 cases in which an adult female was trapped five or more times within 1 year, 26 were trapped at one mound exclusively, 54 were trapped at two mounds, and 47 were trapped at three or more mounds (Jones, 1984).

Males may defend the mound of a female against other males. Thus, there may be little home range overlap between males, or if males do not defend the area of females, there may be extensive overlap between males (Munger et al., 1983). Males are attracted to urine of estrous females, which may provide them with information about the reproductive condition of females (Randall, 1986). They enter the home area of females to mate, and when more than one male is present, males compete for access to the female. Mating patterns include mutual circling and nonlocking copulation with a single mount (Randall, 1987*a*).

Banner-tailed kangaroo rats usually are gentle and timid and depend upon flight and their burrows for protection (Bailey, 1905). However, two *D. spectabilis* in captivity usually fight savagely whenever they are put together (Bailey, 1931). They fight by leaping in the air and striking with the hind feet. Sometimes they carry on a sparring match with their forefeet. Biting, if done at all, is a secondary means of combat (Vorhies and Taylor, 1922).

The forefeet are used in locomotion and in digging. When these kangaroo rats walk, they move in a slow hop, involving the placing of the forefeet on the ground, followed by the forward movement of both hind feet in unison (Howell, 1933). There is little tendency for sudden prolonged immobility, but there is increased heart rate and respiration rate (Hofer, 1970).

Banner-tailed kangaroo rats of both sexes exhibit philopatry. Though weaning occurs at about 1 month of age, offspring share natal burrows with their mothers for 3 to 7 months, and 39% of surviving offspring remain within natal home ranges through reproductive maturity. Data on the availability of burrows and on patterns of resettlement suggest that natal philopatry in this species may be a means of providing juveniles with access to essential resources; that is, food caches and large complex burrow systems that are not available readily outside natal home ranges (Jones, 1984).

Juveniles that acquire parental resources (large complex burrow systems and food caches) are significantly more likely to survive to reproductive age than individuals that successfully disperse, but do not acquire parental resources. Survival of juveniles that leave their natal burrows and move to other burrows is independent of the distance moved, suggesting that familiarity with natal areas and proximity to relatives impart no survival advantage. The frequency of burrow abandonment by adult females is independent of maternal age, and survival of abandoning mothers does not differ from that of nonabandoning females (Jones, 1986).

Dipodomys spectabilis have been evicted from their own burrows by grasshopper mice (*Onychomys*; Bailey, 1940), and they are subordinate to pocket gophers (Geomyidae; Hickman, 1977) and to *D. merriami* (Reichman, 1983). However, Frye (1983) found *D. merriami* was subordinate to *D. spectabilis* and is excluded from home ranges of the larger species during the autumn harvesting season. Fights with other species usually are savage and to the death (Bailey, 1931; Vorhies and Taylor, 1922). Banner-tailed kangaroo rats were the fastest species among seven heteromyids tested at seed-husking, but smaller species were more efficient in dealing with large seeds because they had a smaller metabolic drain (Rosenzweig and Sterner, 1970).

GENETICS. *Dipodomys s. spectabilis*, *D. s. perblandus*, and *D. s. baileyi* have 2n = 72 chromosomes, but differ in chromosomal configuration (Fig. 6). *D. s. spectabilis* has 35 acrocentric chromosomes and a fundamental number of 70; *D. s. perblandus* has four submetacentric chromosomes, 31 acrocentric chromosomes, and a fundamental number of 78; and *D. s. baileyi* has 12 submetacentric chromosomes, 23 acrocentric chomosomes, and a fundamental number of 94. Sex chromosomes also differ (Stock, 1974).

Cesium chloride-buoyant density-peak values for DNA samples of *D. spectabilis* do not differ greatly from 92 other species belonging to 11 orders of mammals (Arrighi et al., 1970). Most satellite DNA is nearly identical to that of other *Dipodomys* (Mazrimas and Hatch, 1972, 1977), and similarity of satellite DNA can be used in phylogenetic comparisons of *D. spectabilis* to other species (Hatch and Mazrimas, 1977; Mazrimas and Hatch, 1977). Based on 17 proteins the mean number of alleles per locus per population is 1.06, the mean proportion of loci polymorphic per population is 0.06, and the mean proportion of loci heterozygous per individual is 0.008 (Johnson and Selander, 1971).

REMARKS. *Dipodomys spectabilis* is most similar to *D. nelsoni* (Best and Schnell, 1974; Grinnell, 1921; Lidicker, 1960; Schnell et al., 1978; Setzer, 1949). *D. nelsoni* apparently was derived from *D. spectabilis* and retains many of the morphologic characteristics of *D. spectabilis* including a diploid chromosomal count of 72. Subspecies of *D. spectabilis* differ from each other chromosomally in the same way they differ from *D. nelsoni*, but to a lesser degree (Stock, 1974). *D. nelsoni* has been regarded as a subspecies of *D. spectabilis* (Nader, 1978), but statistical analyses of morphologic data separate the two (Anderson, 1972; Matson, 1980). In addition, *D. spectabilis* differs from *D. nelsoni* in three burrow characteristics; *D. spectabilis* has fewer total number of openings and number of active openings, and larger diameter of inactive openings (Best et al., 1988). *D. elator* may be closely related to *D. spectabilis* (Davis, 1942), and it may represent the ancestor from which *D. spectabilis* was derived (Stock, 1974). However, genetic data indicate that *D. elator* is more similar to *D. phillipsii* and is markedly divergent from *D. spectabilis* (Hamilton et al., 1987).

Several popular accounts have featured banner-tailed kangaroo rats (Jones and Bush, 1984; Peterson, 1968). *Dipodomys* is from the Greek words *di* (two), *podos* (foot), and *myos* (mouse; Jaeger, 1955), which refer to its enlarged hind feet and bipedal mode of locomotion. Perhaps Merriam (1890) selected the name *spectabilis* because of the size and striking coloration of this species. The first use of "banner-tailed kangaroo rat" was by Allen (1895:212). Bailey (1905) pointed out that it is regrettable that the name "kangaroo rat" became firmly fixed to this group of beautiful jerboa-like rodents that are as unratlike as they are widely removed from the marsupials.

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