Dipodomys deserti Stephens, 1887

Desert Kangaroo Rat

Dipodomys deserti Stephens, 1887:42. Type locality "Mojave River, Cal. [3–4 mi. from, and opposite, Hesperia, San Bernardino Co., California; Hall, 1981:588]."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae. The genus *Dipodomys* contains about 21 species (Honacki et al., 1982). The species contains four subspecies (Hall, 1981):

D. d. aquilus Nader, 1965:52. Type locality "1½ mi. NW High Rock Ranch, T28N–R17E, Sec. 26, about 12 mi. SE Wendel, 4080 ft, Lassen Co., California."
D. d. arizonae Huey, 1955:99. Type locality "3 miles southeast of Picacho, Pinal County, Arizona."
D. d. deserti Stephens, 1887:42, see above (*helleri* Elliot is a synonym).
D. d. sonoriensis Goldman, 1923:139. Type locality "La Libertad Ranch, 30 miles east of Sierra Seri, Sonora, Mexico."

DIAGNOSIS. The desert kangaroo rat (Fig. 1) is among the largest of the genus (Best, in press). The mastoids meet immediately behind the parietals (Fig. 2), having at most an inconspicuous spicule between them; this character distinguishes *D. deserti* from all other species of *Dipodomys*. In addition, *D. deserti* has the flattest skull of any member of the genus (Merriam, 1890).

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). *D. deserti* differs from *D. spectabilis* in the maxillary bridge of the orbit, which is fully one-third broader in *D. spectabilis* (Merriam, 1890).

GENERAL CHARACTERS. *Dipodomys deserti* possesses externally opening, fur-lined cheek pouches that are used to transport

seeds (Eisenberg, 1975). There are four toes on each hind foot and the foot is covered with relatively long hairs (Nader, 1978). The tail amounts to 143% of the length of head and body or about 58% of the total length. A ventral, dark tail-stripe usually is absent. The distal one-third of the tail is crested and the long hairs of the crest
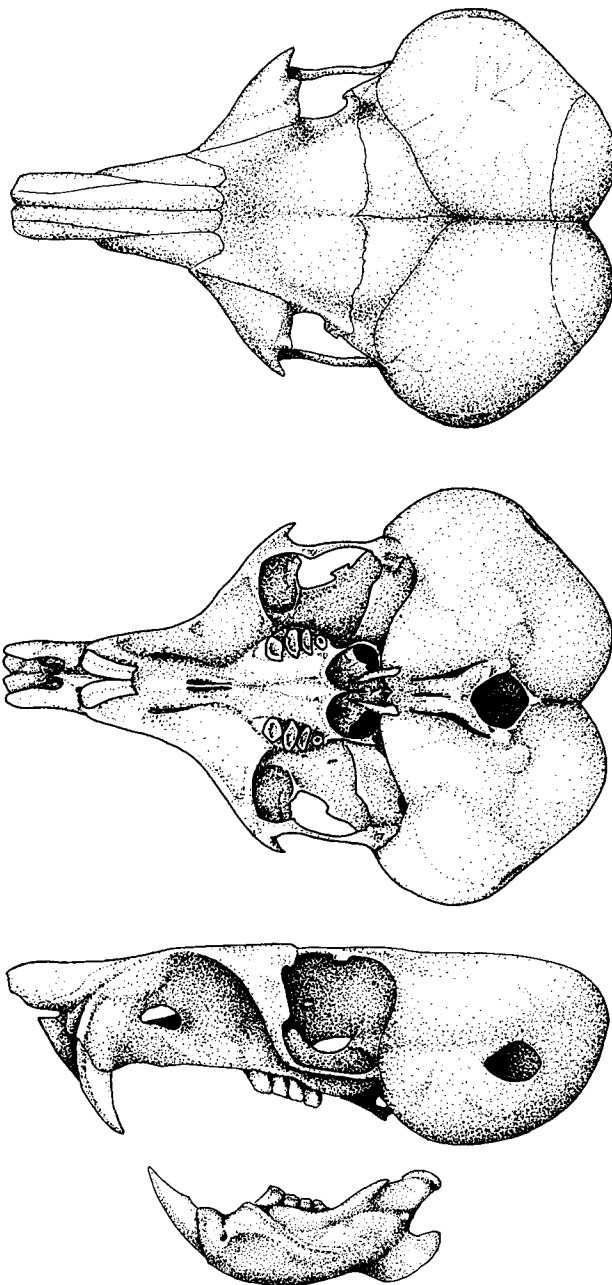

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Dipodomys deserti* (Texas Tech University 38332, male, 15 mi. SE Victorville, San Bernardino Co., California). Greatest length of cranium is 46.7 mm. Drawings by S. O. MacDonald.

FIG. 1. *Dipodomys deserti arizonae* from 4 mi. S, 1 mi. E Picacho, Pinal Co., Arizona. Photograph by W. W. Goodpaster.
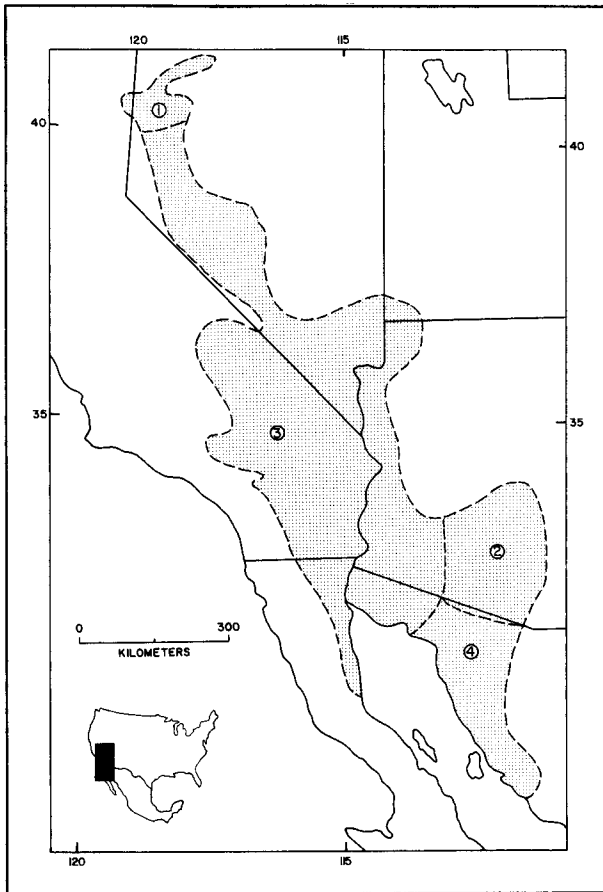
FIG. 3. Distribution of *Dipodomys deserti* in southwestern North America (Hall, 1981): 1, *D. d. aquilus*; 2, *D. d. arizonae*; 3, *D. d. deserti*; 4, *D. d. sonoriensis*.

are dusky, except that the distal 25 mm of the tail is white (Hall, 1946).

The venter, forelimbs from elbow, and hind limbs in front, from knee, are white. There is an indistinct white spot over the eye, another behind the ear that extends across the shoulder to the white underparts. In addition, there is an indistinct white band across the hips and an indistinct darker spot at the base of the whiskers. Soles of the hind feet are nearly white (Stephens, 1887). The color of the upper parts varies from pale fawn to grayish black, depending on the subspecies. In the zone of integradation between 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 (Nader, 1978).

Juvenile pelage is like that of the adult, except it is shorter and less dense; the tail is less heavily tufted. The dark interval toward the end of the tail is blacker, the white tip shorter, and sometimes there is a distinct ventral tail stripe leading about halfway from the base to the white tip (Grinnell, 1922).

Mean measurements (in mm) of 254 adult males and 204 adult females, respectively, from throughout the range of the species are: total length, 342.4 and 330.7; length of body, 141.2 and 135.5; length of tail, 201.1 and 195.2; length of hind foot, 53.7 and 52.6; length of ear, 15.9 and 15.5; basal length of cranium, 24.7 and 24.0; greatest length of cranium, 45.8 and 44.7; maxillary arch spread, 23.9 and 23.1; interorbital width, 12.4 and 12.2; nasal length, 17.1 and 16.6; intermaxillary width, 8.3 and 8.1; alveolar length, 6.0 and 5.9; lacrimal length, 4.3 and 4.2; maxillary arch width, 4.8 and 4.6; basioccipital length, 6.6 and 6.5; greatest depth of cranium, 15.2 and 14.9; greatest width of cranium, 30.6 and 29.9; zygomatic width, 21.7 and 21.2; and nasal width, 4.2 and 4.1 (Best, in press). Mass of adult males ranges from 91.0 to 148.0 g and from 82.8 to 141.2 g for adult females (Nader, 1978).

Males average 2.5% larger than females in skeletal measures

and about 7% more in mass (Hall, 1946). *D. deserti* is one of the most sexually dimorphic species of kangaroo rats. Males are significantly larger in 17 of 19 characters, including total length, length of tail, length of hind foot, greatest length of cranium, maxillary arch spread, nasal length, greatest depth of cranium, and greatest width of cranium (Best, in press).

Geographic variation among populations is not great. This may be because *D. deserti* inhabits almost uniform terrain (loose sandy soil) and because there are no geographic barriers within the range. The most variable morphologic characters are total length, length of body, greatest length of cranium, and greatest breadth across bullae. The least geographically variable measurements are length of hind foot, rostral width, breadth across maxillary arches, and basal length (Nader, 1978).

DISTRIBUTION. The desert kangaroo rat occupies the most arid region of southwestern North America (Fig. 3). It inhabits all of the dunes within its geographic and elevational range, including several southern dunes where it is the only species present (Brown and Lieberman, 1973). The only potential geographic barrier within its range is the Colorado River (Nader, 1978). However, the river is no permanent barrier to *D. deserti* (Goldman, 1937). Elevations occupied range from −60 m at Salt Creek, Death Valley National Monument, Inyo Co., California, to 1,710 m in the Huntoon Valley, Mineral Co., Nevada (Nader, 1978).

FOSSIL RECORD. There is no fossil record of this species. However, *D. deserti* probably originated in the early Pleistocene in the southwestern United States; most probably in southeastern California and the lower Colorado Desert (Nader, 1978).

FORM AND FUNCTION. This species is the most highly specialized of any *Dipodomys*. The bullae are huge, and frequently meet in the center of the dorsal surface of the skull, completely hiding the interparietal and supraoccipital. The maximum width of interparietal is 0.3 mm (mean = 0.12; Wood, 1935). The interparietal is variable in the number of bones composing it; there is one bone present in 41.3%, two in 6.4%, three in 3.2%, and no interparietal in 49.2% of specimens (Beer, 1965). The supraoccipitals, tympanics, and mastoids are inflated (Wood, 1935). Volume of the mastoid bullae is 3,496 mm^3 and the relative bullar inflation (bullar volume/total volume of skull) is 0.53 (Kotler, 1984b).

The infraorbital foramen is an elongated canal that is buried in the side of the rostrum. The sphenopterygoid canal is reduced to a foramen for a large vein; the vascular canal is vestigial. The foramen ovale, through which the mandibular nerve leaves the cranium, is confluent with the foramen lacerum. The canal for the internal carotid artery is not separable from the elongate jugular foramen, which is large and slit-like (Hill, 1935).

The tooth enamel is thick and reaches a maximum of 0.30 mm; this is at least 20% greater than in any other *Dipodomys*. There are no grooves at the sides of the teeth. The lower fourth premolar is the last tooth to develop interrupted enamel. The lower incisors are without sulci and are slightly rounded on their anterior faces. The masseteric ridge is high, folded up over the masseter, and slants upward anteriorly (Wood, 1935). These molariform teeth are non-evergrowing and closure of the bases commences in subadults. In general, the bases of the roots of the molars close before those of the premolars; the bases close earlier in the lower fourth premolar than in the upper (Nader, 1966). In *D. deserti* and *D. spectabilis*, the crowns of the teeth are worn away with greater rapidity than in any of the other species. As these are both large species, there may be a connection between size and rate of destruction of the teeth (Wood, 1935).

The hyoid apparatus consists of only two parts, 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 (Nader, 1978).

In fresh pelage, the greatest lengths (in mm) of hairs are: rump, 24; top of head, 14; belly, 12; chin, 6; ears, 3; hind toes, 5; basal half of tail, 2.5; tuft of tail, 31; longest vibrissae, 71 (Grinnell, 1922). *D. deserti* has the longest hair in the family and it has some of the thickest hair for the genus. Mean length of hair is 19.1 mm (range, 18.5 to 20.6) and mean width is 0.030 to 0.048 mm. The base is wide; shaft curved; tip tapers gradually; cross-section slightly flattened oval; medulla cells oval to flattened; and there are rows of medulla cells that sometimes are regular, one cell alternating with

two or three cell rows (Homan and Genoways, 1978). Pelage is in the most worn condition in summer (Grinnell, 1922). Except for November and December, some are in the process of molting every month. There seems to be only one molt per year, occurring in the spring and summer, with a peak in July (Nader, 1978).

A holocrine skin gland is located mid-dorsally. It is an area of enlarged and modified sebaceous glands. Glandular area epidermis and dermis are thickened; elastic fibers, mast cells, capillaries, and melanophores are particularly abundant in the dermal partitions between gland units (Quay, 1954). Secretion by the gland is nearly uniform in the sexes and continuous throughout the year. The size of the gland is greatest from April to June and in November and December; possibly related to molt or reproduction (Quay, 1953). This scab-like gland is prominent during parturition (Butterworth, 1964). Sebaceous and mucous glands are present at the oral lips and angle (Quay, 1965).

The thyroid secretes thyroxine at a rate of 0.96 μg/100 g of body mass. Thyroxine-binding occurs essentially in the albumin zone (Yousef and Johnson, 1975). Plasma thyroxine level is 45 ng/ml (Scott et al., 1976). Mean hemoglobin concentration/mean hematocrit is 33.5 (Lee and Brown, 1970).

Except for *D. deserti* and *D. nitratoides*, generally there is a significant relationship between bacular and body lengths in *Dipodomys* (Best, 1981). However, the baculum of this large-sized kangaroo rat is the smallest in the genus (Best and Schnell, 1974). The basal end of the baculum is slightly enlarged and somewhat higher than wide; it tapers gradually into the shaft, and the distal end is turned up at nearly a right angle (Burt, 1960). Mean measurements (in mm) are: length, 9.49; height of base, 1.25; and width of base, 1.04 (Best and Schnell, 1974). The baculum has a roundness of base (dorso-ventral/lateral diameter of base) of 1.30, an index of robustness (dorso-ventral diameter of base + lateral diameter of base × 100/length) of 22.4, and a relative length (body length/baculum length) of 15.47 (Lidicker, 1960b).

The mammae are arranged in three pairs, two inguinal and one pectoral (Burt, 1934). These three pairs of mammae, normally pink and invisible in the hair, become long, tapered, and deep red during nursing. The hair is parted from around them. The inguinal nipples appear to have the greatest use. The mammae of the female gradually regress and disappear in the hair of the venter (Butterworth, 1964).

Dipodomys deserti has several adaptations for ricochetal locomotion (Hatt, 1932) including: shortening of forelimbs and neck; strengthening of iliosacral joint; increase in length of hind foot; reduction or loss of side digits of hind foot; increase in strength and complexity of long back muscles; elongation of tail; tuft on end of tail; compacting of viscera; and increased size of eye (Eisenberg, 1963). Speed of travel is 1.56 m/s, or 5.6 km/h. Length of hops is about 58 cm; leap-lengths are 62 to 67 cm. Footprints in sandy soil are 18 to 20 mm across the toes. The heel rarely shows at all. Hind footprints are side by side, though one may be slightly behind the other (Grinnell, 1937).

Mean total surface area of the body is 255.0 cm² and mean relative surface area (total surface area/mass) is 2.25 cm²/g (Lawler and Geluso, 1986). The individual cheek pouch volume is 2.77 cm³ (Morton et al., 1980). Skeletal indices include: humeroradial, 149.5; intermembral, 53.4; crural, 139.4; tibioradial, 54.9; femorotarsalmetatarsal, 96.6; and cranial, 67.6. *D. deserti* has an average specialization of 9.6; it is the most specialized species in the genus. Visceral measurements (in mm) are: length of large intestine, 397; length of small intestine, 195; and percent of small to large intestine, 49.2 (Setzer, 1949).

The brain has an extremely prominent superior olivary complex. The medial superior olive is so large that it extends deep to the pons and there is a small lateral olive (Webster, 1969). The mean endocranial volume is 1.68 cc. Of the 212.8 mm² dorsal surface area of the brain, 72% is cerebrum, 21% is cerebellum, and 7% is olfactory bulbs (Hafner and Hafner, 1984).

The ear shows electrical responses to sounds from 100 to 20,000 cycles/s and the most sensitive range is from 2,000 to 4,000 cycles/s (Katsuki and Davis, 1954). The middle ear has the following dimensions (in mm unless otherwise indicated): volume, 1.41 cm³; relative volume, 0.27 cm³; tympanic membrane diameter, 7.10; length of stapes footplate, 1.80; width of stapes footplate, 0.98; length of malleus, 3.85; and length of incus, 1.21 (Webster and Webster, 1975). The auditory system has hypertrophied Hensen's cells with long apical processes supporting and forming an

elevated reticular lamina. These Hensen's cells reach their maximum size in the upper second and lower third turns; throughout they rest on inner Claudius' cells rather than the basilar membrane (Webster and Webster, 1980).

The volume of oxygen consumed at rest in the thermoneutral zone averages 0.87 ml g⁻¹ h⁻¹ (Yousef and Johnson, 1975). The rate of oxygen consumption as a function of speed is 0.66 × speed + 3.25 (Thompson et al., 1980). The maximum oxygen consumption estimated during bipedal hopping is 8.26 ml g⁻¹ h⁻¹ (Thompson, 1985). *D. deserti* has a low basal metabolic rate and a low thermal conductance. Low basal rates are an alternative to the production of concentrated urine as a means of reducing water turnover, and low conductance compensates for low rates of metabolism (McNab, 1979).

Gross anatomy of the kidney is similar to other small rodents, but the papilla are relatively long and extend into the ureter. The diameter of the Malpighian body is 85 to 105 μ. The glomerulus is lobulated. The outer diameter of the proximal tubule is about 30 μ, and the lining cells of the first part of the proximal tubule are especially rich in basal rods. A brush border is distinct. The thin segment of Henle's loop has an outer diameter of 10 to 15 μ. The distal convoluted tubule has a lumen of about 17 μ and an outer diameter of 27 μ (Vimtrup and Schmidt-Nielsen, 1952). Means of renal indices are: relative medullary thickness = 10 (absolute medullary thickness)/cube root of the product of the absolute measurements of the length by width by thickness of the kidney, 7.21; percent medullary thickness = 100 (medullary thickness/cortical + medullary thicknesses), 85.0; ratio of inner medullary zone to cortex = thickness of inner medullary zone/cortical thickness, 4.47; ratio of medulla to cortex = medullary thickness/cortical thickness, 5.69 (Lawler and Geluso, 1986).

Desert kangaroo rats drink water freely when it is available (Butterworth, 1964), but can survive long periods on a dry diet. A regression analysis of metabolic water production/evaporative waterloss equals 2.150 (0.954) at an ambient temperature of 16.2°C and a mean mass of 104.7 g (MacMillen and Hinds, 1983). The mean exchangeable body-water content measured by the tritium water-dilution method is 62.4% of the body mass. On a barley diet, the mean turnover times for exchangeable body water varies from 13.9 to 22.1 days (Richmond et al., 1960). When sodium chloride and urea are introduced into the bladder of water-deprived *D. deserti*, there is no change in volume or changes in urea or salt concentrations (Schmidt-Nielsen and Schmidt-Nielsen, 1952).

This species does not hibernate. Torpor (when body temperature and energy metabolism are reduced well below normothermic levels) is only weakly developed (MacMillen, 1983).

A few hours after copulation, a gelatinous plug forms in the vaginal orifice. This plug persists for several days. Apparently there are two types of plugs; one derived after copulation and another less-durable type that is derived from the sloughed lining of the internal genital tract. Both types indicate reproductive activity (Butterworth, 1961b).

ONTOGENY AND REPRODUCTION. *Dipodomys deserti* has been bred in captivity. The gestation period is 29 to 32 days (Butterworth, 1961b) and the number of embryos ranges from one to six with a mean of 3.43 and a mode of 3.0. One or possibly two litters (February and May) are produced each year (Nader, 1978). The success or failure of reproduction closely follows the success of winter annuals (Beatley, 1976b).

Reproductive activity begins early in January and continues through early July. The first recorded pregnancy is 18 January (three embryos 30 mm in length) and the latest reproductive activity is lactation on 10 July, with pregnancies every month between. February has the largest number of pregnant females and the largest number of young born, judged from the number of embryos. No differences are detectable in the time of pregnancy between northern and southern populations (Nader, 1978). Adult females come into estrus 10 to 15 days post-partum and accept males. Females in diestrus resist precopulatory advances of males (Butterworth, 1964).

Mass at birth is 3.04 g (range, 2.2 to 4.6; Haley, 1964) and a newborn is about 52 mm in total length (Nader, 1978). At birth *D. deserti* is naked with a thin, pink, transparent skin. The abdominal organs are visible through the skin of the venter, and the sutures and blood vessels on the skull can be seen. After 5 days black pigmentation appears on the dorsum and top of the head, and a faint dorsal tail stripe is also seen. Complete pigmentation and furring

with the adult color pattern appears at 21 days. At birth the snout area containing the vibrissal sheaths is richly vascular and swollen. The vibrissa are 6 mm long at birth, 13 mm at 5 days, 23 mm at 15 days, and 72 mm at 90 days. The growth rate of *D. deserti* is slower than that of *D. merriami*, but at 30 days both reach one-half of their adult body mass. The fastest growing portion of the anatomy is the foot. At 15 days, the feet of *D. deserti* reach 70% of adult size. At birth, *D. deserti* can crawl; quadrupedal locomotion is well developed by 9 days and hopping locomotion occurs by 11 days. The vagina opens between 24 and 33 days and scrotal testes appear in 85 days. Other developmental characters (in days) include: eyes open, 11 to 17; ears open, 9 to 15; incisors erupt, 7 to 10; solid food eaten, 15; solid feces appear, 15; nails harden, 12 to 15; cleaning of pelage with sand, 17; fully haired, 11 to 15; weaning, 15 to 25 days; mammae visible, 21; drumming with feet, 33; full ear growth, <90; full tail growth, <90; full foot growth, 50 to 90; fully mature, 90; attain adult body mass, 150 to 180; and reach adult total length, 97 (Butterworth, 1961a; Haley, 1964). They begin to use their cheek pouches at 21 days (Butterworth, 1964).

Sexual maturity begins early in life. In five immature females, one was lactating and another had four embryos; among 23 subadults, 10 were pregnant (Nader, 1978). One *D. deserti* lived for 5 years and 5 months in captivity (Brattstrom, 1960) and another for at least 8.5 to 9 years (Nader, 1978).

ECOLOGY. The desert kangaroo rat is adapted to live in the lowest, hottest, and most arid regions of North American deserts (Nader, 1978). It is closely restricted to areas where accumulations of wind-driven sand have reached considerable depths. Elsewhere it is present sparingly or not at all; it may live in silty ground where the soil becomes flour-like (Grinnell, 1937). *D. deserti* is less abundant near the edges of dunes where the sand is shallower and creosotebushes (*Larrea*) are closer together (Johnson et al., 1948). It is known to occur in gravelly soil only in one locality; near Florence in central Arizona (Nader, 1978).

In the Mojave Desert, the distribution of *D. deserti* is correlated with the low shrub cover and low mean precipitation/mean temperature ratios of *Larrea* communities. Mean values (range in parentheses) of attributes of the habitat occupied by *D. deserti* here include: precipitation, 124.3 mm (117.0 to 130.3); maximum temperature, 29.0°C (28.0 to 29.9); minimum temperature, 0.3°C (−3.2 to 2.3); temperature, 14.6°C (13.2 to 16.2); mean precipitation/mean temperature ratio, 8.5 (7.3 to 9.7); cover of shrubs, 17.2% (10.7 to 22.1); height of shrubs, 29.5 cm (22.1 to 40.6); cover of perennial grasses, 1.5% (0 to 2.5); cover of herbaceous perennials (other than grasses), 0.3% (0.1 to 1.1); cover of winter annuals, 5.9% (0.8 to 11.5); and cover of summer annuals, 0.3% (0 to 1.3; Beatley, 1976a).

Contrary to other large species of *Dipodomys*, *D. deserti* occurs in areas that receive little precipitation. Perhaps to compensate for the lack of precipitation, *D. deserti* is restricted to sand-dune habitats that may be richer in food resources than surrounding habitats. Food resources may be concentrated in dune areas by the action of surface winds (Munger et al., 1983).

In California, desert kangaroo rats occur in areas with sparse vegetation, dominated by *Larrea tridentata*, *Hilaria rigida* (Thompson, 1985), *Fouquieria*, *Franseria*, and several varieties of *Opuntia* and *Yucca* (Eisenberg, 1963). In Nevada, the dominant vegetation on the sand-dunes is *Sarcobatus vermiculatus*, *Atriplex canescens* (Kotler, 1984a), and *Artemisia* (Eisenberg, 1963).

Mounds used as sites for burrows often are in open spaces, but usually are under vegetation (Johnson et al., 1948). Burrows are not made in areas of most rapidly shifting dunes and may be plugged with dirt. Widths and heights of four burrow openings (in mm) are: 130 by 60; 75 by 95; 110 by 85; and 65 by 70 (Grinnell, 1937). On the surface, the burrow is a lumpy, uneven area, 3 to 9 m across, into which numerous sloping entrances lead down to a labryinth of passages winding to a depth of 0.3 to 1.2 m. The underground network includes a number of storerooms and a nest that is a roughly spherical chamber filled with dry grasses, chaff, and vegetable down (Ketcham, 1940). These animals store large quantities of mesquite (*Prosopis*) pods and other seeds in underground cavities (Elliot, 1904).

The desert kangaroo rat may form widely-spaced colonies consisting of clusters of 6 to 12 large burrows in each. Occasionally an isolated burrow is seen. The colonies are abandoned from time to time; few colonies persist for a long period of time. Perhaps these

kangaroo rats establish their colonies near patches of seed-bearing plants, utilize the food source until it is exhausted, then abandon their colonies and move to a new location where seeds are still present. Shifting sand and cave-ins may lead them to abandon their burrows, but often old, inactive burrows are found that have remained intact (Ryan, 1968).

In Deep Canyon, California, only 15 holes in a total of 104 burrows showed signs of being used (Ryan, 1968). At a set of 6 to 12 burrow openings, only two appeared to be used during one night. Near each set of openings there appear several miniature sinks 0.3 to 0.6 m across that may be made by caving in of the burrows. Fresh, well-beaten trails, ordinarily two, leading in opposite directions and averaging 12.7 cm wide, extend out from each set of burrows. At one burrow a trail was 68 m long and the one in the opposite direction was even longer. The paths turn aside for bushes and other obstructions, but as a rule they run in nearly straight lines and are conspicuous features (Hall, 1946).

The desert kangaroo rat does not eat succulent green plants, even when available. They will pass through the green plants to feed upon partially buried, dried plants from the previous year (Ryan, 1968). However, cheek pouches of one collected in Nevada contained green vegetation that included: seeds of *Larrea*, leaves of *Artemisia*, and fragments of stem and fruiting capsule of Scrophulariaceae (probably *Penstemon*; Burt, 1934). Cheek pouches of another contained seeds and heads of *Glyptopleura marginata* and seeds of *Lupinus*. Another contained leaves and flower heads of *Gilia leptomeria* and leaves of *Atriplex* (Hall, 1946). Cheek pouches of a female in Death Valley, California, contained hardened sap of mesquite (*Prosopis*; Grinnell, 1937). Seeds collected ranged in size from 1.40 to >4.70 mm (Brown, 1975).

In Death Valley, California, populations are about 0.5/ha (Grinnell, 1937). In Deep Canyon, California, populations/ha varied from 0.17 (28 to 30 March), to 1.44 (28 to 30 October), to 3.04 (3 to 5 February; Ryan, 1968). In the Mojave Desert of Nevada, *D. deserti* makes up only about 1% of the rodent fauna (Beatley, 1976a). However, the desert kangaroo rat is an important member of any dune community where it is present (Brown, 1973). Species that coexist with *D. deserti* include *Perognathus amplus*, *P. longimembris*, *P. parvus*, *Chaetodipus penicillatus*, *Microdipodops megacephalus*, *M. pallidus*, *D. merriami*, *D. microps*, *D. ordii* (Brown, 1975), *D. panamintinus* (Nader, 1978), *Reithrodontomys megalotis*, *Peromyscus crinitus*, *P. maniculatus* (Brown, 1975), *P. truei* (Kotler, 1984b), *Onychomys torridus*, *Neotoma lepida* (Kotler, 1985b), *Ammospermophilus leucurus* (Ketcham, 1940), *Lepus californicus*, and *Canis latrans* (Ryan, 1968). In Arizona, *D. deserti* may share its burrow with *Spermophilus tereticaudus* and *Sylvilagus audubonii* (Hoffmeister, 1986).

Where *D. deserti* and *D. merriami* coexist, they both forage in the open, but *D. deserti* harvests larger seeds (Brown, 1975). Microhabitat utilization measured by traps and by tracks do not differ significantly for *D. deserti*, *D. merriami*, and *M. pallidus* (Kotler, 1985a). In laboratory trials, the amount of seed harvested by *P. longimembris* or *M. pallidus* is limited if *D. deserti* is present; death of one of these small species is a likely outcome of such interactions (Trombulak and Kenagy, 1980).

Predators include "fox, coyote, bobcat, hawk, snake, and small spotted skunk" (Ketcham, 1940:542). Other predators include long-eared owls (*Asio otus*), kit foxes (*Vulpes macrotis*), and gopher snakes (*Pituophis melanoleucus*; Kotler, 1984b).

Some interactions with humans are harmful to *D. deserti*. Vehicles passing over the highways of southeastern California exact enormous tolls each year, to the point of almost eliminating the species along a wide area on either side of the pavement (Huey, 1941). Conversely, at the Nevada Test Site these kangaroo rats are found in loose and sandy soil entirely in areas that have evidence of disturbance, particularly manmade disturbance such as dikes (Jorgensen and Hayward, 1965). Also, cultivating the land in northwestern Arizona has worked to the advantage of the desert kangaroo rat because removal of the native cover has permitted the winds to pile up quantities of fine sand. These animals do not live in the area immediately under cultivation, but along it, and as soon as cultivation stops, they re-invade the area (Hoffmeister and Durham, 1971).

The desert kangaroo rat can be experimentally infected with human influenza virus (Eaton et al., 1941). Although *D. deserti* have been examined, no coccidians have been recovered (Hill and Best, 1985). However, they can be artificially infected with *Eimeria mohavensis* (Doran, 1953). Helminth parasites include *Cateno-*

taenia linsdalei, Heteromxyurus deserti, Protospirura dipodomis, and *Rectularia dipodomis.* Mites include *Hyponeocula deserticola, Echinonyssus triacanthus, Ischyropoda armatus, Geomylichus deserti, Dermadelema furmani, Euschoengastoides arizonae,* and *Hexidionis deserti.* Ticks include *Ixodes pacificus.* Lice include *Fahrenholzia pinnata.* Fleas include *Meringis dipodomys, M. deserti, M. cummingi, Aetheca wagneri, Foxella ignota, Malaraeus telchinus,* and *Oropsylla aridis* (Whitaker, in press).

BEHAVIOR. Though the desert kangaroo rat is nocturnal (Grinnell, 1937), they often are out of their burrows in daytime (Johnson et al., 1948). They will kick sand out of the burrow during the daytime, plug entrances to the burrow, open up others, and dig new tunnels (Ketcham, 1940).

No burrow has more than one occupant at a time, except in the case of a female with young (Ketcham, 1940). The species is extremely solitary and drives away all animals that invade its territory (Butterworth, 1964). *D. merriami* retreats from the larger and more aggressive *D. deserti.* Retreat always begins before any physical contact takes place and *D. deserti* shows little or no interest in pursuit (Congdon, 1974). When individual Mongolian gerbils (*Meriones unguiculatus*) were placed into the cage of *D. deserti,* the desert kangaroo rat neither feared nor fought the gerbils. A few brief skirmishes were lost, but *D. deserti* was never submissive (Fisler, 1977).

Sand is kicked at objects to determine whether they are alive or dangerous. *D. deserti* will kick sand onto traps in sufficient quantities to spring them or to bury them (Benson, 1935).

During surface foraging and in the initiation of new tunnels, loose soils, such as dry, fine sand are moved by pulling small piles of soil between the hind feet using both front limbs simultaneously. These motions are similar to those of the forelimbs during high-speed pouching of seeds. When a sufficient pile of soil has accumulated under the body, the hind limbs are used to kick the sand further back. Soil may be moved underground by turning around and pushing the soil with forelimbs and chest. This method is used to move soil up a tunnel ramp preparatory to plugging the entrance. The soil is then patted into place with rapid alternating movements of the forefeet. The frequency of such movements is 8.23 strokes/s; the digging cycle averages 5.27 strokes/s (Nikolai and Bramble, 1983).

Desert kangaroo rats dust and bathe in the sand. This activity helps keep their fur clean and free of grease (Hoffmeister, 1986). Sandbathing consists of several well-integrated movements. Initially the animal digs rapidly with its forepaws. It then lowers its cheek to the sand and extends its body while sliding forward on its side. Alternative extension and flexion of the body results in a series of side-rubs. In other cases, the extension and flexion may be performed with the venter pressed against the sand; in this instance the movement is termed ventral-rub. Generally, an animal will perform isolated side-rubs or ventral-rubs, but an extended sequence of sandbathing usually includes both acts (Eisenberg, 1964). Sides are alternated during sandbathing (Eisenberg, 1967).

Dipodomys deserti has been observed caching seeds in captivity (Eisenberg, 1963), but little is known of the food-caching habits. Buried seeds are detected at depths of 20 cm when surface seeds are present. During two nights, 10,481 g of seed were removed by presumably two *D. deserti.* Generally, seeds taken were high in carbohydrates; those left were high in proteins. The seeds with high carbohydrates that were taken had a carbohydrate to protein ratio >2.0, a carbohydrate to oil ratio of >15.0, and either a thin seed coat or completely hulled (Lockard and Lockard, 1971).

Approximately 60% of tracks are in the open (Kotler, 1985a). Trapping data indicate they forage at least 2 m from plants in the most open area of bare sand (Brown and Lieberman, 1973). However, based upon other field observations, they concentrate their foraging efforts (>75%) near or beneath the canopies of shrubs. They frequently traverse open areas at high speeds and search for large clumps of seeds (Thompson, 1982). The cruising radius in one night may reach hundreds of meters. The seeds produced over large areas are accessible by this behavior (Grinnell, 1937).

Mean movement between foraging locations is 7.52 m: duration of movement, 2.04 s; speed, 6.28 km/h; modal speed, 6.00 to 6.49 km/h (range, 0.54 to 26.66). The mean distance from the burrow to the first foraging stop is 10.49 m; duration of the movement, 1.48 s; speed, 7.45 km/h (range, 3.33 to 15.45); distance from the last foraging stop to the burrow, 10.96 m; duration of the movement, 0.86 s; speed, 12.95 km/h (range, 7.31 to 22.21).

Mean foraging time/night is 138 min; 71% of this time is spent slow foraging (Thompson, 1985). While foraging, the mean number of digs and gleans/min is 5.00; number of stops/min, 6.38; speed of slow foraging, 1.25 km/h; speed of transit, 6.33 km/h; number of shrubs visited/foraging bout, 8.7 (Thompson, 1982).

The high-speed pouching of seeds by *D. deserti* is stereotyped. Both forelimbs move in synchrony and each limb serves only the ipsilateral pouch. During the pouching cycle, the first digit is used in semi-opposable fashion. The pouching cycle of the forelimbs is attended by synchronized mandibular movements. Seed pouching is rapid, with a mean pouching rate of millet seed of 9.01 cycles/s. Some cycles are executed in <90 ms. Depending on how many seeds are grasped in each hand, pouching rates range between approximately 20 and 60 millet seeds/s. Unacceptable items are not recognized and rejected while in the hands. Instead, pouch items are quickly tested for suitability before pouching by being pinched between the pursed lips or between the lower incisors and the lips. Pinching of food may be a consequence of coupling mandibular motion to forelimb movement. Those items judged unacceptable are retrieved from the front end of the pouch and thrown backward beneath the animal (Nikolai and Bramble, 1983). *D. deserti* has a slightly higher rate of pouching mistakes than *C. penicillatus.* Harvest rates increase with decrease in size of soil particles (Price and Heinz, 1984).

Adults of both sexes will build nests in captivity. Juveniles may construct individual nests soon after weaning. Nests are enlarged constantly and used for sleeping and breeding. When nests are moved to a new location, nesting material is transferred in the cheek pouches (Butterworth, 1964).

No definitive courtship period exists because of their intense aggressive behavior. A short precopulatory period, when the two sexes are compatible, is immediately related to the sexual act. The female does not tolerate the advances of the male until the proper condition of estrus has occurred. During this period she presents herself to the male. Frequently she drags her genital region in the sand as if cleaning herself. In seeking out the male, she first faces him and then turns her genital region to him. The male noses her genital organs and occasionally bites the base of her tail. This behavior continues until the male effects copulation. During copulation, the male mounts the female posteriorly, grasping her pelvic region tightly with his forelimbs. He also holds the skin of her neck with his teeth. The female digs nervously in the sand with her front feet during copulation, but makes no attempt to escape. The actual sex act varies in length from one to several minutes and movements are relatively slow. The male rocks clumsily back and forth, using his tail as a brace that prevents him from falling over backwards. This motion brings the scrotum in contact with the ground and causes the scrotal area to become irritated and red. A few hours after copulation a gelatinous plug develops in the vaginal orifice and she no longer tolerates the advances of the male (Butterworth, 1961b).

Females sit on their hind legs during parturition. They close their eyes slightly during the abdominal contractions. Young are born head first; the female assists delivery by pulling at the fetal membranes. The newborn are suspended by their umbilical cords and are dragged over the sand until the cords break. Females move their nose and mouth to their inguinal region, examine and clean the vaginal orifice, but make no attempt to bite or sever the umbilical cords. The young push their feet against the abdomen of the female while attached. There is no trace of an amnion or placenta. The entire process takes 15 to 45 min. After delivery, the female cleans herself. Young frequently are retrieved by picking them up with the mouth. The female continuously kicks sand onto the newborn animals; the sand may dry them. The female is quite active during delivery, but afterward stands over the litter and sleeps for several hours. Before the eyes of the young open, the mother attacks intruders and frequently licks the young clean of feces, urine, and other materials. After the young open their eyes, the mother rarely moves them or interferes with their activities. She occasionally brings food into the nest (Butterworth, 1964).

Females stand on their hind legs while nursing, spreading their bodies as widely as possible. The young rest on their backs extending their feet into the air gently kicking the venter of their mother as they nurse. When disturbed, females with nursing young attached to their nipples jump from the nest spilling or pulling the juveniles with them. In hot weather, females lie on their backs while the young rest on the venter as they nurse. After the eyes of juveniles are fully open, they nurse less each day (Butterworth, 1964).

FIG. 4. Karyotype of *Dipodomys deserti* (Hsu and Benirschke, 1975).

Females react when disturbed by trying to move young from one nest to another. Moving is accomplished by grasping the young across the middle of the back or behind the head with her mouth, hopping away with one animal, and then returning for another. The jaws of the female nearly encompass the body of the young; the forelimbs are used for balance and to assist in carrying the young. After about 21 days, juveniles are left to care for themselves. Females may cover young with nesting material when they must leave the nest. Males may exhibit paternal behavior and may be gentler with the young than the mother. Older juveniles may chase adult males out of food areas by biting and pulling at their pelage (Butterworth, 1964).

Nonvocal auditory communication includes footdrumming and possibly tooth-chattering. *D. deserti* drums more, and in a more stereotyped fashion, than any other species of kangaroo rat. Footdrumming may be slow (2.4 beats/s; when an animal is exploring a new environment), fast (about 10 beats/s; when an animal is suddenly startled), or a roll (5 beats/0.33 s interval; employed at unspecific intervals during a bout of slow drumming; Eisenberg, 1963). They begin to drum or stamp their hind feet as early as 30 days after birth and employ this behavior throughout their life (Butterworth, 1964). Following copulation, both sexes kick sand in short swift strokes, drum, and thump the ground with their hind feet (Butterworth, 1961b).

Desert kangaroo rats may squeal, grunt, make a low, chucking sound, or give a purring growl. Young cry like newborn puppies (Ketcham, 1940) and have soft, squeaking voices that are used continuously. Voices are used less as animals grow to maturity. Early in life they begin to make a growling purr when picking up food; this habit extends into adult behavior (Butterworth, 1964). A similar purr is emitted throughout copulation by the female; the male is silent (Butterworth, 1961b).

These kangaroo rats are excellent swimmers; their large hind feet give them considerable agility in the water (Stock, 1972). However, the inundation of their habitat during floods along the Beaverdam Wash in southwestern Utah probably restricts their movement upstream and accounts for their paucity of numbers in that area (Durrant, 1943).

When handled they will not bite, unless forcibly held. They rapidly lose their fear of humans (Ketcham, 1940). Desert kangaroo rats have been subjects of zoo exhibits (Dolan and Moran, 1969).

GENETICS. Cells of *D. deserti* contain less DNA than those of *D. ordii* (Hori and Lark, 1974). The nuclear DNA content for *D. deserti* is 8.8 pg (Hatch et al., 1976). The percent of the total area under an analytical ultracentrifuge scan of ultraviolet absorbance in neutral cesium-chloride density gradients indicates the following proportions of DNA components in *D. deserti*: principal, 37; intermediate, 44; and two satellite DNA components totaling 19% (Mazrimas and Hatch, 1972). Conditions for optimal separation of DNA in density gradients for *D. deserti* are: initial density, 1.523 g/ml; M ratio of Ag$^+$/DNA-P, 0.24; μg AgNO$_3$/μg DNA, 0.125.

The strand densities for a given satellite DNA are nearly identical among species of *Dipodomys* (Mazrimas and Hatch, 1977).

The liver esterases may be useful in evaluating phylogenetic variation of rodents (Holmes and Massaro, 1969). Protein analysis revealed the mean number of alleles/locus for four populations was 1.06, the mean proportion of loci polymorphic/population was 0.06, and the mean proportion of loci heterozygous/individual was 0.010; intermediate in variation among 11 species of *Dipodomys* examined (Johnson and Selander, 1971).

The fundamental number of chromosome arms is 108 (Fig. 4). There are 3 metacentric chromosomes, 16 submetacentrics, 4 subtelocentrics, 8 acrocentrics and telocentrics, the X chromosome is submetacentric, and the Y chromosome is acrocentric-subtelocentric (Stock, 1974).

REMARKS. *Dipodomys* is from the Greek words *di* (two), *podos* (foot), and *myos* (mouse; Jaeger, 1955) that refer to its enlarged hind feet and bipedal mode of locomotion. The name *deserti* refers to the arid habitat where this species occurs.

Attempts have been made to arrange kangaroo rat species into groups to show phylogenetic relationships. The first attempt was that of Grinnell (1921), who placed *D. deserti* into a group alone. Subsequent studies to elucidate relationships between *D. deserti* and other species of *Dipodomys* have considered: skeletal and visceral measurements (no close affinities; Setzer, 1949); field experience (*D. elator, D. nelsoni*, and *D. spectabilis*; Lidicker, 1960a); structure of the molariform teeth (*D. heermanni, D. merriami, D. nitratoides*, and *D. ordii*; Nader, 1966); protein variation (*D. merriami* and *D. nitratoides*; Johnson and Selander, 1971); percent of satellite DNA compared to indices derived from lengths of limb bones (*D. spectabilis*; Mazrimas and Hatch, 1972); percent of satellite plus intermediate DNA and the fundamental number of chromosome arms (*D. microps* and *D. nitratoides*; Mazrimas and Hatch, 1972); bacula (*D. merriami, D. panamintinus*, and *D. phillipsii*; Best and Schnell, 1974); chromosomes (*heermanni* group; Stock, 1974); immunologic distance (an outlier; Hatch and Mazrimas, 1977); phenetic analyses of skeletal characters (an outlier, but its closest affinity is with *D. ingens* and *D. spectabilis*; Schnell et al., 1978); and phenetic analyses of cranial characters (*D. ingens, D. nelsoni*, and *D. spectabilis*; Best, in press).

LITERATURE CITED

BEATLEY, J. C. 1976a. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. J. Mamm., 57:67–93.

———. 1976b. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. Oecologia, 24:21–42.

BEER, J. R. 1965. The interparietal in kangaroo rats. Southwestern Nat., 10:145–150.

BENSON, S. B. 1935. A protective habit of Dipodomys deserti. J. Mamm., 16:67–68.

BEST, T. L. 1981. Bacular variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Southwestern Nat., 25:529–534.

———. In press. Patterns of morphologic and morphometric variation in heteromyid rodents. *In* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Spec. Publ., Amer. Soc. Mamm., 10.

BEST, T. L., AND G. D. SCHNELL. 1974. Bacular variation in kangaroo rats (genus Dipodomys). Amer. Midland Nat., 91: 257–270.

BRATTSTROM, B. H. 1960. Longevity in the kangaroo rat. J. Mamm., 41:404.

BROWN, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology, 54:775–787.

———. 1975. Geographical ecology of desert rodents. Pp. 315–341, *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard Univ. Belknap Press, Cambridge, Massachusetts, 545 pp.

BROWN, J. H., AND G. A. LIEBERMAN. 1973. Resource utilization

and coexistence of seed-eating desert rodents in sand dune habitats. Ecology, 54:788–797.

BURT, W. H. 1934. The mammals of southern Nevada. Trans. San Diego Soc. Nat. Hist., 7:375–428.

———. 1960. Bacula of North American mammals. Misc. Publ. Mus. Zool., Univ. Michigan, 113:1–76.

BUTTERWORTH, B. B. 1961a. A comparative study of growth and development of the kangaroo rats, Dipodomys deserti Stephens and Dipodomys merriami Mearns. Growth, 25:127–139.

———. 1961b. The breeding of Dipodomys deserti in the laboratory. J. Mamm., 42:413–414.

———. 1964. Parental relations and the behavior of juvenile kangaroo rats (Dipodomys) in captivity. Southwestern Nat., 8:213–220.

CONGDON, J. 1974. Effect of habitat quality on distributions of three sympatric species of desert rodents. J. Mamm., 55:659–662.

DOLAN, J. M., AND M. MORAN. 1969. Historical list of Mammalia exhibited in the San Diego Zoological Garden. Der Zool. Garten, 37:48–63.

DORAN, D. J. 1953. Coccidiosis in the kangaroo rats of California. Univ. California Publ. Zool., 59:31–60.

DURRANT, S. D. 1943. Dipodomys deserti in Utah. J. Mamm., 24:404.

EATON, M. D., W. P. MARTIN, AND J. C. TALBOT. 1941. Susceptibility of kangaroo rats to strains of human influenza virus. Proc. Soc. Exp. Biol. Med., 48:181–182.

EISENBERG, J. F. 1963. The behavior of heteromyid rodents. Univ. California Publ. Zool., 69:1–100.

———. 1964. A comparative study of sandbathing behavior in heteromyid rodents. Behaviour, 22:16–23.

———. 1967. A comparative study in rodent ethology with emphasis on evolution of social behavior, I. Proc. U.S. Natl. Mus., 122:1–51.

———. 1975. The behavior patterns of desert rodents. Pp. 189–224, in Rodents in desert environments (I. Prakash and P. K. Ghosh, eds.). Dr. W. Junk Publ., The Hague, Monogr. Biol., 28:1–624.

ELLIOT, D. G. 1904. Catalogue of mammals collected by E. Heller in southern California. Field Columbian Mus. Publ. 91, Zool. Ser., 3:271–321.

FISLER, G. F. 1977. Potential behavioral dominance by the Mongolian gerbil. Amer. Midland Nat., 97:33–41.

GOLDMAN, E. A. 1923. Three new kangaroo rats of the genus Dipodomys. Proc. Biol. Soc. Washington, 36:139–142.

———. 1937. The Colorado River as a barrier in mammalian distribution. J. Mamm., 18:427–434.

GRINNELL, J. 1921. Revised list of the species in the genus Dipodomys. J. Mamm., 2:94–97.

———. 1922. A geographical study of the kangaroo rats of California. Univ. California Publ. Zool., 24:1–124.

———. 1937. Mammals of Death Valley. Proc. California Acad. Sci., Fourth Ser., 23:115–169.

HAFNER, M. S., AND J. C. HAFNER. 1984. Brain size, adaptation and heterochrony in geomyoid rodents. Evolution, 38:1088–1098.

HALEY, T. J. 1964. Experimental usefulness of the kangaroo rat. Lab. Anim. Care, 14:95–102.

HALL, E. R. 1946. Mammals of Nevada. Univ. California Press, Berkeley, 710 pp.

———. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1–600 + 90.

HATCH, F. T., A. J. BODNER, J. A. MAZRIMAS, AND D. H. MOORE, II. 1976. Satellite DNA and cytogenetic evolution DNA quality, satellite DNA and karyotypic variations in kangaroo rats (genus Dipodomys). Chromosoma, 58:155–168.

HATCH, F. T., AND J. A. MAZRIMAS. 1977. Satellite DNA and cytogenetic evolution: molecular aspects and implications for man. Human Cytogen., ICU-UCLA Symp. Molecular Cell. Biol., 7:395–414.

HATT, R. T. 1932. The vertebral columns of ricochetal rodents. Bull. Amer. Mus. Nat. Hist., 63:599–738.

HILL, J. E. 1935. The cranial foramina in rodents. J. Mamm., 16:121–129.

HILL, T. P., AND T. L. BEST. 1985. Coccidia from California kangaroo rats (Dipodomys spp.). J. Parasitol., 71:682–683.

HOFFMEISTER, D. F. 1986. Mammals of Arizona. Univ. Arizona Press and Arizona Game and Fish Dept. [Tucson], 602 pp.

HOFFMEISTER, D. F., AND F. E. DURHAM. 1971. Mammals of the Arizona Strip including Grand Canyon National Monument. Tech. Ser., Mus. N. Arizona, 11:1–44.

HOFFMEISTER, D. F., AND I. A. NADER. 1963. Distributional notes on Arizona mammals. Trans. Illinois State Acad. Sci., 56:92–93.

HOLMES, R. S., AND E. J. MASSARO. 1969. Phylogenetic variation of rodent liver esterases. J. Exp. Zool., 172:323–334.

HOMAN, J. A., AND H. H. GENOWAYS. 1978. An analysis of hair structure and its phylogenetic implications among heteromyid rodents. J. Mamm., 59:740–760.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Assoc. Syst. Coll., Lawrence, Kansas, 694 pp.

HORI, T. A., AND K. G. LARK. 1974. Autoradiographic studies of the replication of satellite DNA in the kangaroo rat. Autoradiographs of satellite DNA. J. Molec. Biol., 88:221–232.

HSU, T. C., AND K. BINIRSCHKE (EDS.). 1975. An atlas of mammalian chromosomes. Vol. 9, Folio no. 408, Springer-Verlag, New York, unpaged.

HUEY, L. M. 1941. Mammalian invasion via the highway. J. Mamm., 22:383–385.

———. 1955. A new race of Dipodomys and a new race of Thomomys from Arizona. Trans. San Diego Soc. Nat. Hist., 12:99–102.

JAEGER, E. C. 1955. A source-book of biological names and terms. Charles C Thomas Publ., Springfield, Illinois, 323 pp.

JOHNSON, D. H., M. D. BRYANT, AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. Univ. California Publ. Zool., 48:221–376.

JOHNSON, W. E., AND R. K. SELANDER. 1971. Protein variation and systematics in kangaroo rats (genus Dipodomys). Syst. Zool., 20:377–405.

JORGENSEN, C. D., AND C. L. HAYWARD. 1965. Mammals of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser., 6(3):1–81.

KATSUKI, Y., AND H. DAVIS. 1954. Electrophysiological studies of ear of kangaroo rat (Dipodomys). J. Neurophysiol., 17:308–316.

KETCHAM, W. E. 1940. Dipo, the little desert "kangaroo." Nat. Geog. Mag., 78:537–548.

KOTLER, B. P. 1984a. Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. J. Mamm., 65:91–96.

———. 1984b. Risk of predation and the structure of desert rodent communities. Ecology, 65:689–701.

———. 1985a. Microhabitat utilization in desert rodents: a comparison of two methods of measurement. J. Mamm., 66:374–378.

———. 1985b. Owl predation on desert rodents which differ in morphology and behavior. J. Mamm., 66:824–828.

LAWLER, R. M., AND K. N. GELUSO. 1986. Renal structure and body size in heteromyid rodents. J. Mamm., 67:367–372.

LEE, A. K., AND J. H. BROWN. 1970. Variations in the hemoglobin concentrations of Great Basin rodents. J. Mamm., 51:669–674.

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

———. 1960b. The baculum of Dipodomys ornatus and its implication for superspecific groupings of kangaroo rats. J. Mamm., 41:495–499.

LOCKARD, R. B., AND J. S. LOCKARD. 1971. Seed preference and buried seed retrieval of Dipodomys deserti. J. Mamm., 52:219–221.

MACMILLEN, R. E. 1983. Adaptive physiology of heteromyid rodents. Great Basin Nat. Mem., 7:65–76.

MACMILLEN, R. E., AND D. S. HINDS. 1983. Water regulatory efficiency in heteromyid rodents: a model and its application. Ecology, 64:152–164.

MAZRIMAS, J. A., AND F. T. HATCH. 1972. A possible relationship between satellite DNA and the evolution of kangaroo rat species (genus Dipodomys). Nature New Biol., 240:102–105.

————. 1977. Similarity of satellite DNA properties in the order Rodentia. Nucleic Acids Res., 4:3215–3227.

McNab, B. K. 1979. Climatic adaptation in the energetics of heteromyid rodents. Comp. Biochem. Physiol., 62A:813–820.

Merriam, C. H. 1890. Descriptions of three new kangaroo rats, with remarks on the identity of Dipodomys ordii of Woodhouse. N. Amer. Fauna, 4:41–49.

Morton, S. R., D. S. Hinds, and R. E. MacMillen. 1980. Cheek pouch capacity in heteromyid rodents. Oecologia, 46:143–146.

Munger, J. C., M. A. Bowers, and W. T. Jones. 1983. Desert rodent populations: factors affecting abundance, distribution, and genetic structure. Great Basin Nat. Mem., 7:91–116.

Nader, I. A. 1965. Two new subspecies of kangaroo rats, genus Dipodomys. Proc. Biol. Soc. Washington, 78:49–54.

————. 1966. Roots of teeth as a generic character in the kangaroo rats, Dipodomys. Bull. Biol. Res. Centre, Baghdad, 2:62–69.

————. 1978. Kangaroo rats: intraspecific variation in Dipodomys spectabilis Merriam and Dipodomys deserti Stephens. Illinois Biol. Monogr., 49:1–116.

Nikolai, J. C., and D. M. Bramble. 1983. Morphological structure and function in desert heteromyid rodents. Great Basin Nat. Mem., 7:44–64.

Price, M. V., and K. M. Heinz. 1984. Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. Oecologia, 61:420–425.

Quay, W. B. 1953. Seasonal and sexual differences in the dorsal skin gland of the kangaroo rat (Dipodomys). J. Mamm., 34:1–14.

————. 1954. The dorsal holocrine skin gland of the kangaroo rat (Dipodomys). Anat. Rec., 119:161–175.

————. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. J. Mamm., 46:23–37.

Richmond, C. R., T. T. Trujillo, and D. W. Martin. 1960. Volume and turnover of body water in Dipodomys deserti with tritiated water. Proc. Soc. Exp. Biol. Med., 104:9–11.

Ryan, R. M. 1968. Mammals of Deep Canyon Colorado Desert, California. Desert Mus., Palm Springs, California, 137 pp.

Schmidt-Nielsen, K., and B. Schmidt-Nielsen. 1952. Water metabolism of desert mammals. Physiol. Rev., 32:135–166.

Schnell, G. D., T. L. Best, and M. L. Kennedy. 1978. Interspecific morphologic variation in kangaroo rats (Dipodomys): degree of concordance with genic variation. Syst. Zool., 27:34–48.

Scott, I. M., M. K. Yousef, and H. D. Johnson. 1976. Plasma thyroxine levels of mammals: desert and mountain. Life Sci., 19:807–812.

Setzer, H. W. 1949. Subspeciation in the kangaroo rat, Dipodomys ordii. Univ. Kansas Publ., Mus. Nat. Hist., 1:473–573.

Stephens, F. 1887. Description of a new species of Dipodomys, with some account of its habits. Amer. Nat., 21:42–49.

Stock, A. D. 1972. Swimming ability in kangaroo rats. Southwestern Nat., 17:98–99.

————. 1974. Chromosome evolution in the genus Dipodomys and its taxonomic and phylogenetic implications. J. Mamm., 55:505–526.

Thompson, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology, 63:1303–1312.

————. 1985. Bipedal hopping and seed-dispersion selection by heteromyid rodents: the role of locomotion energetics. Ecology, 66:220–229.

Thompson, S. D., R. E. MacMillen, E. M. Burke, and C. R. Taylor. 1980. The energetic cost of bipedal hopping in small mammals. Nature, 287:223–224.

Trombulak, S. C., and G. J. Kenagy. 1980. Effects of seed distribution and competitors on seed harvesting efficiency in heteromyid rodents. Oecologia, 44:342–346.

Vimtrup, B., and B. Schmidt-Nielsen. 1952. The histology of the kidney of kangaroo rats. Anat. Rec., 114:515–528.

Webster, D. B. 1969. Comparative morphology of the superior olivary complex in Heteromyidae. Amer. Zool., 9:1148–1149.

Webster, D. B., and M. Webster. 1975. Auditory systems of Heteromyidae: functional morphology and evolution of the middle ear. J. Morphol., 146:343–376.

————. 1980. Auditory systems of Heteromyidae: cochlear diversity. J. Morphol., 152:153–170.

Whitaker, J. O., Jr. In press. Parasites of heteromyid rodents. In Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Spec. Publ., Amer. Soc. Mamm., 10.

Wood, A. E. 1935. Evolution and relationships of the heteroymid rodents with new forms from the Tertiary of western North America. Ann. Carnegie Mus., 24:73–262.

Yousef, M. K., and H. D. Johnson. 1975. Thyroid activity in desert rodents: a mechanism for lowered metabolic rate. Amer. J. Physiol., 229:427–431.

T. L. Best, Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station, Auburn University, Alabama 36849-5414; N. J. Hildreth and C. Jones, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock 79409.