Dipodomys deserti, 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 Dipodomynae. The genus *Dipodomys* contains about 21 species (Hosacki et al., 1982). The species contains four subspecies (Hall, 1981):

- *D. d. aquillus* 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. deserti* Stephens, 1887:42, see above (*helleri* Elliot is a synonym).
- *D. d. somoriensis* 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 34% of the total length. A ventral, dark tail-ring usually is absent. The distal one-third of the tail is crested and the long hairs of the crest

![Fig. 1. *Dipodomys deserti arizonae* from 4 mi. S, 1 mi. E Picacho, Pinal Co., Arizona. Photograph by W. W. Goodpaster.](image1)

![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.](image2)
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, 1987). The color of the upper parts varies from pale fawn to grayish black, depending on the subspecies. In the zone of integration 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).

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 24.4; greatest length of cranium, 34.8 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; basiocpical 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 (hose 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 supraocciptals, tympanics, and mastoids are inflated (Wood, 1935). Volume of the mastoid bullae is 3.496 mm³ and the relative bullar inflation (bullar volume/total volume of skull) is 0.53 (Kotler, 1944).

The infraorbital foramen is an elongated canal that is buried in the side of the rostrum. The sphenosphenoid 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 maseteric ridge is high, folded up over the maseter, 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-June, some are in the process of molting or moult. 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. desertii and D. nitratoides, generally there is a significant relationship between basal and body weights in Dipodomys (Best, 1981). However, the basculum of this large-sized kangaroo rat is the smallest in the genus (Best and Schnell, 1974). The basal end of the basculum is slightly enlarged and somewhat higher than wide; it tapers gradually into the shaft, and the distal end is turned slightly right angle (Butterworth, 1974). Mean measurements (in mm) are: length, 9.49; height of base, 1.25; and width of base, 1.04 (Best and Schnell, 1974). The basculum has a roundness of base ( dorso-ventral diameter of base) of 1.30, an index of robustness ( dorso-ventral diameter of base + lateral diameter of base x 100), of 22.4, and a relative length (body length/basculum length) of 15.47 (Lidicker, 1966b).

The mammary 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 mammary of the female gradually regress and disappear in the hair of the venter (Butterworth, 1964).

Dipodomys desertii has several adaptations for ricochetal locomotion (Hatt, 1932) including: shortening of forelimbs and neck; strengthening of basioccipital joint; increase in length of hind foot; reduction or loss of side digits of hind foot; increase in strength and complexion of long back muscles; elongation of tail; tuft on end of tail; compacting of visera; and increase size of eye (Eisenberg, 1958). Length of hind foot is 1.56 mm/s, body mass is 0.173 g, length of height of base is about 38 cm, length-peak lengths are 62 to 617 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 258.0 cm2 and mean relative surface area (total surface area/mass) is 2.25 cm2/g (Lawler and Gelso, 1986). The individual cheek pouch volume is 2.77 cm3 (Morton et al., 1980). Skeletal indices include: humeroradial, 149.5; intermembran, 33.4; crural, 139.4; thoriodaral, 54.9; femorotarsal, 96.6; and cranial, 67.6. D. desertii 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 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 mm3 dorsal surface area of the brain, 72% is cerebrum, 21% is cerebellum, and 7% is olfactory bulb (Hafner and Hafner, 1954).

The electrical recording from 10 to 15 days post-partum and accept males. Females in diestrus resist prepuberal advances of males (Butterworth, 1964). Mass at birth is 3.04 g (range, 2.2 to 4.6; Hale, 1964) and a newborn is about 52 mm in total length (Nader, 1978). At birth D. desertii is naked with a thin, pink, transparent skin. The abdominal organs are visible through the skin of the venter, and the sprints and blood vessels on the skin can be seen. After 5 days black pigmentation appears on the dorsum and top of the head, and a dark ventral tail stripe is also seen. Complete pigmentation and furring of

The volume of oxygen consumed at rest in the thermoneutral zone averages 0.87 ml g·h⁻¹ (Yousef and Johnson, 1975). The rate of oxygen consumption as a function of speed is 0.66 x speed + 3.25 (Thompson et al., 1980). The maximum oxygen consumption estimated during bipedal hopping is 8.26 ml g·h⁻¹ (Thompson, 1985). D. desertii 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, 1970).

The 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 (Vintrop and Schmid-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 thickness), 85.9; 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 Gelso, 1986).

Dessert kangaroo rats drink water freely when it is available (Butterworth, 1964), but can survive long periods of total dry diet. A regression analysis of metabolic water production/evaporative water loss 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. desertii, 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 lasts 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).

ONTGENY AND REPRODUCTION. Dipodomys desertii 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, 1976).

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 breeding season. The presence of sex sounds from 10 to 15 days post-partum and accept males. Females in diestrus resist prepuberal advances of males (Butterworth, 1964). Mass at birth is 3.04 g (range, 2.2 to 4.6; Hale, 1964) and a newborn is about 52 mm in total length (Nader, 1978). At birth D. desertii is naked with a thin, pink, transparent skin. The abdominal organs are visible through the skin of the venter, and the sprints and blood vessels on the skin 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 vibrissa sheaths is richly vascular and swollen. The vibrissa are 6 mm long at birth, 13 mm at 5 days, 25 mm at 10 days, and 30 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 serial 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 180b; and reach adult total length, 97 (Butterworth, 1961a; Hale, 1940). They begin to use their cheek pouches at 21 days (Butterworth, 1964).

The 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 (Bratstrom, 1960) and another for at least 6.5 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 the region of sand dunes and 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 creosoted bushes (Ellisoria) are closer together (Johnson et al., 1940), to 1,440 ft. 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, 14.0°C (13.2 to 16.2); mean precipitation/mean temperature ratio, 0.5 (0.7 to 1.1); cover of shrub, 17.2% (10.7 to 22.1); height of shrubs, 29.5 cm (22.1 to 40.5); cover of perennial grasses, 1.5% (0.0 to 2.5); cover of herbage perennial (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% (0.0 to 1.3; Beal, 1928).

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 sanddune 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, Frasera, and several varieties of Opuntia and Yucca (Eisenberg, 1963). In Nevada, the dominant vegetation on the sand-dunes is Sarothamnus 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 lump, uneven area, 3 to 9 m across, into which numerous sloping entrances lead down to a labyrinth of passages ranging in size at 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 caches (Kotler, 1984a).

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 burrows and form new colonies nearby when the food is 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 burrows 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 21.5 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, check 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). Check pouches of another contained heads of Glycyphylloides marginata and seeds of Lupinus. Another contained leaves and flower heads of Gilia leptomeria and leaves of Atriplex (Hall, 1946). Check pouches of a specimen in Death Valley contained hard-seeded sap of Prosopis (Prosopis; Grinnell, 1937). Seeds collected ranged in size from 1.40 to 2.70 mm (Brown, 1975).

In Death Valley, California, populations are about 0.5/ha (Grinnell, 1937). In Deep Canyon, California, populations varied from 0.17 (28 to 30 March) to 0.34 (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 Pslocercus leucopus, Tympanoctomys tigermensis, 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. manueli (Brown, 1975), P. truei (Kotler, 1984a), Ochotona torrida, Neotoma lepida (Kotler, 1985a), Anomospermophilus leucurus (Ketcham, 1940), Lepus californicus, and Canis latrans (Ryan, 1968). In Arizona, *D. deserti* may share its burrow with Spermophilus tereticaudus and Sylvilagus audoboni (Hoffmeister, 1988).

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 *D. 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, 1984a).

Some interactions with humans are harmful to *D. deserti*. Vehicles passing over the highways of southwestern California exact enormous tolls each year, to the point of almost eliminating the species over a wide area on either side of the pavement (Fluey, 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 mammade disturbance such as dikes (Jorgensen and Hayward, 1965). Also, cultivating the land in northwestern Arizona has worsened the problem, since 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 (Hall and Best, 1985). However, they can be artificially infected with *Eimeria mohavensis* (Doran, 1935). Helminth parasites include _Catenacolubris_ species 339.
MAMMALIAN SPECIES 339
taenia linsdalei, Heteromyxurus deserti, Protopsorura dipodomis, and Rectangularia dipodomis. Mites include Hypoconoctes deserticola, Echigotamus, Jackoia, and Arachnocampa. Of the species, Desert deserts, Desertdesert, Desert Desert, Desert deserts, the only one to be found in the desert is D. deserti. D. deserti was collected from open grasslands along the borders of desert areas.

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 day, and when it is dark, they will open up their burrows and dig them 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 after any physical contact takes place and D. deserti shows little or no interest in pursuit (Loudon, 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 brief brief skinnishes were lost, but D. deserti was never submissive (Fisher, 1977).

Sand is kicked at objects to determine whether they are alive or dangerous. D. deserti will kick sand onto traps in sufficient quantity to discourage the animals or to bury them (Minnis, 1935).

During sand-finding and in the initiation of new tunnels, 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 pole vaulting 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 sand with the forelimbs and chest. This method is used to move soil up a tunnel ramp preparatory to plugging the entrance. The soil is then placed into the burrow with the hind limbs alternately moving the soil to the front of the foot. The frequency of such movements is 8.25 strokes/sec; the digging cycle averages 5.27 strokes/sec (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. Then it 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 forelimbs together as if the animal were to kick sand. A similar movement is termed ventral rubbing. Generally, an animal will perform isolated side-rubs or ventral-rubs, but an extended sequence of sandbathing usually includes both acts (Eisenberg, 1964). Side-rubs 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 cm when surface seeds are present. During two nights, 10,481 g of seeds 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, 1980a). Trapping data indicate they forage for at least 2 cm 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 cranial 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/hr; modal speed, 6.00 to 6.49 km/hr (range, 5.45 to 6.66). The distance from the foraging stop is 10.49 m; duration of movement, 1.48 s; speed, 7.45 km/hr (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/hr (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 seeds and number of seeds in each hand, foraging rates vary between 1.25 km/hr; speed of transportation, 6.33 km/hr; 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-oppositional fashion. The pouching cycle of the forelimbs is attended by synchronized mandibular movements. Seed pouching is rapid, with a mean pouching rate of miller seed of 9.01 cycles/sec. Some cycles are executed in <0.9 ms. Depending on how many seeds are grasped in each hand, pouching rates range between approximately 20 and 60 miller seeds/sec. Unacceptable seeds 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. Pouching of food may be a consequence of a coupling mandibular motion to forelimb movement. Those items judged unacceptable are retrieved from the front end of the pouch and thrown away towards the animal (Nikolai and Bramble, 1983). D. deserti has a slightly higher rate of pouching mistakes than C. pustulatus. 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 elevated constantly and used for sleeping and breeding. When nests are moved, the female is seen near or in the nest material that is transferred in the check pouches (Butterworth, 1964).

No definitive courtship period exists because of their intense aggressive behavior. A short prelude to mating is only mating, which is immediately related to the sexual act. The female is usually in estrus for a long period of time and the 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 area with the lower lip and the female is then available for copulation. This behavior continues until the male achieves 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 vigorously 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 him. This motion brings the scrotum in contact with the ground and causes the seminal vesicles to be stretched and released. At the same time, 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 unibical cords and are dropped over the sand until the cords break. Females move their nose and mouth to their inginal region, examine and clean the vaginal orifice, and 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 animal. 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 lifts 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 in the air gently kicking the venter of their mother as they nurse. When directly between the female's breasts from 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* (Heu and Beinischke, 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 unspecified 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, shallow strokes, drum, and thump the ground with their hind feet (Butterworth, 1961b).

Desert kangaroo rats may squeal, grunt, make a low, chuckling 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 growing 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 AgNO₃/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/focus 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 Grimnell (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. heermannii, D. merriami, D. nitratoides, and D. ordii*; Niator, 1960); 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. panaminitius, and D. phillipian*; Best and Schnell, 1974); chromosomes (*heermannii* group; Stock, 1974); immunologic distance (an outlier; Hatch and Mazrimas, 1977); phenetic analyses of skeletal characteristics (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).

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