MAMMALIAN SPECIES No. 377, pp. 1-7, 5 figs.

Dipodomys ingens.

By Daniel F. Williams and Kerry S. Kilburn

Published 12 April 1991 by The American Society of Mammalogists

Dipodomys ingens (Merriam, 1904)

Giant Kangaroo Rat

Perodipus ingens Merriam, 1904:141. Type locality "Painted Rock, 20 [=25.5] miles southeast of Simmler, Carrizo Plain, San Luis Obispo Co., California."

Dipodomys ingens: Grinnell, 1921:95. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae, Genus *Dipodomys*. Currently, 21 Recent species are recognized in the genus (Williams and Genoways, in press). *Dipodomys ingens* is monotypic (Grinnell, 1922).

DIAGNOSIS. *Dipodomys ingens* (Fig. 1) is the largest kangaroo rat, having the greatest length of head and body (means of 55 males and 47 females are 147.6 and 144.5 mm, respectively; Best, in press). It can be distinguished from the other large-sized kangaroo rats (*D. deserti*, *D. nelsoni*, and *D. spectabilis*) by presence of five, rather than four, toes on each hind foot. From the sympatric kangaroo rats, *D. heermanni* and *D. nitratoides*, *D. ingens* can be distinguished by a length of hind foot >47 mm (means for males and females are 50.2 and 49.2, respectively). The hind feet of *D. heermanni* usually are < 45 mm (means of 474 males and 366 females are 43.3 and 42.6, respectively; Best, in press). The huge hind feet (rarely as short as 46 mm) distinguish even juveniles from other sympatric species. The hind foot of *D. nitratoides* has four toes and its length does not exceed 39 mm (Grinnell, 1922). The skull of *D. ingens* is large and broad (Fig. 2), averaging 26.6-27.0 mm across the maxillary arches, a width much greater than that of other kangaroo rats except *D. spectabilis*, which averages from 25.8 to 26.9 mm (Best, in press; Grinnell, 1922; Nader, 1978). The average greatest length of the skull of *D. ingens* (44.2-45.9 mm; Best, in press; Grinnell, 1932) is equaled only by *D. deserti* and *D. spectabilis* (Nader, 1978). Other diagnostic traits of giant kangaroo rats are their moderately-sized ears, wide maxillary arches (mean width at midlength, 6.2-6.4 mm), and short tails (length of tail is about 128% of length of head and body; range, 112-135%; Grinnell, 1922).

GENERAL CHARACTERS. The giant kangaroo rat, as other species of the genus, is adapted for bipedal, ricochetal locomotion (Eisenberg, 1963). The hind limbs are large compared to the size of the forelimbs, the neck is short, the head is large and flattened, and the eyes and ear pinnae are placed dorsolaterally. The tail is longer than the head and body, conspicuously thickened, and has a dorsal crest of long hairs distally, terminating in a large tuft. The claws on both the forefeet and hind feet are stout (Fig. 1). Large, fur-lined cheek pouches open on each side of the mouth. The pouches extend as deep, invaginated pockets of skin along the sides of the head (Grinnell, 1922; Williams, in press).

The coloration of *D. ingens* is similar to that of other species of kangaroo rats. The dusky-colored nose and vibrissae patches are separated. The cheeks are whitish and the eyelids are completely blackish. The lateral white stripes along the tail are only slightly narrower than the dorsal and ventral dark stripes. The tail tuft is dark in appearance because of a mix of pale and dark hairs. The hairs of the ventral surfaces of the body are pure white to their bases. The buff-colored hairs of the sides and dorsum are mixed with fewer, scattered blackish and dusky hairs. The flanks have a darker appearance caused by more dusky hairs. Juveniles are paler and grayer than adults, the general body color of which is "warm buff" (Grinnell, 1922).

Means of external measurements (in mm) for 15 males and 7 females, respectively (Grinnell, 1932), followed by ranges of measurements (in parentheses; Hall, 1981) are as follows: total length, 332.9, 334.4 (311-348); length of tail, 181.2, 185.7 (157-198); length of hind foot, 50, 50 (46-55). Crown length of ear is about 13 mm. Length of ear from notch averages 17.0 mm (16.0-18.5) for 13 males and 16.7 (15.0-18.0) for 5 females (Grinnell, 1932), and 15.9 mm for 55 males and 15.3 for 47 females (Best, in press). Means and ranges of cranial measurements from Grinnell (1932), based upon 15 adult males and 7 females, respectively, from Panoche Creek, Fresno Co., California, are: greatest length of skull 45.9 (44.0-47.5), 45.1 (43.6-46.0); breadth of skull across bullae, 29.5 (28.1-30.4), 29.0 (28.4-30.0); width across maxillary arches, 27.0 (26.2-28.3), 27.1 (26.5-27.5); greatest length of nasals, 17.1 (16.3-18.0), 17.0 (16.2-17.4); greatest width of rostrum near end, 4.9 (4.6-5.4), 4.6 (4.4-4.8); width of maxillary arch at middle, 6.2 (5.5-7.0), 6.4 (6.0-6.7).

Males ($n = 55$) are significantly larger than females ($n = 47$) in length of body, length of hind foot, basal length of cranium, greatest length of skull, basioccipital length, greatest depth of cranium, greatest width of cranium, and nasal width. There are no significant differences between sexes in 11 other external and skull characters (Best, in press).

Giant kangaroo rats appear to average lighter in weight in habitats supporting lower densities; mass also fluctuates with season, being greatest in winter (January-March) and least from August to October (Williams, in press). Grinnell (1932) reported a mean mass for 15 adult males of 157.0 g (140.0-174.2) and 151.4 (130.8-180.0) for 7 adult females. The lightest female was pregnant, but the heaviest was not. Six adults weighed by Shaw (1934) averaged 148 g (125-159). Specimens in both studies were collected in Fresno County, near the northern limit of the geographic range, in areas supporting continuous populations with high densities over thousands of hectares. For animals living in a small and less-dense colony on the Carrizo Plain, San Luis Obispo Co., California, in August, males and females averaged 114.1 and 108.7 g, respectively; and for 20 weighed in spring, means were 116.2 g for males and 115.0 g for females (Braun, 1983). Williams (in press) recorded weights from 112 to 137 g for animals captured on the Carrizo Plain in August.

The dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. The upper incisors have a vertical groove on their anterior faces (Fig. 2). The anterior faces of the lower incisor are smooth. The molars and premolars are not ever-growing and cusps on their occlusal surfaces are worn away early in life (Wood, 1935).

DISTRIBUTION. The historical distribution of *D. ingens* (Fig. 3) encompasses a narrow band of gentle slopes along the western

FIG. 1. Photograph of a giant kangaroo rat (*Dipodomys ingens*) from Carrizo Plain, San Luis Obispo County, California. Photograph by S. E. B. Hill.

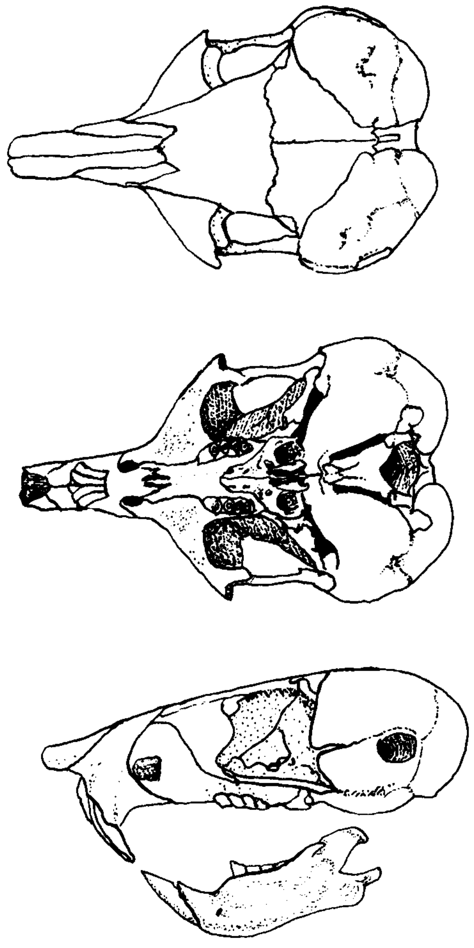

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Dipodomys ingens*. Greatest length of skull is 45.3 mm. Views of skull redrawn from Grinnell (1922; male, Museum of Vertebrate Zoology 14447). Mandible drawn from uncataloged male (D. F. Williams 4588).

edge of the San Joaquin Valley, California. Records of occurrence extend from the base of the Tehachapi Mountains on the south to a point about 16 km south of Los Banos, Merced Co. Inhabited areas west of the San Joaquin Valley include the Carrizo and Elkhorn plains west of the Temblor Mountains, and the upper Cuyama Valley, adjacent to and nearly contiguous with the Carrizo Plain, and scattered colonies in the Ciervo, Kettleman, Panoche, and Tumey hills, and the Panoche Valley (Grinnell, 1922; Hall, 1981; Williams, in press).

Until the late 1960s and early 1970s, little land within the geographic range of *D. ingens* was cultivated or otherwise developed. With completion of the canals of the State Water Project and the San Luis unit of the Central Valley Project, irrigation water became available to the west side of the Tulare Basin, the principal habitat of giant kangaroo rats. Between about 1970 and 1979, nearly all land on the floor of the Tulare Basin was developed for irrigated agriculture, restricting occurrence of most species of the San Joaquin saltbush community, including *D. ingens,* to isolated units in the area of Elk Hills, Kern Co.; Kettleman Hills, Fresno Co.; the southern portions of the Carrizo and Elkhorn plains; and other smaller units at scattered sites in the hills fringing the west side of the Tulare Basin (Williams, in press).

Its distribution as of 1979 (Williams, in press) comprised <2% of the area bounded by historic localities. Even before cultivation of lands within the range, it had a spotty distribution, being absent from large areas of seemingly suitable ground (Grinnell, 1932). Thus, the estimated decline in extent of habitat in recent years probably was overstated. The only colony to be nearly continuously distributed over several square kilometers in 1985 was located on the Elkhorn and Carrizo plains in western San Luis Obispo County. Other colonies extant in 1985 varied from two or three individuals to several thousand individuals in a few areas. Most colonies, however, occupied areas from <1 to 5 ha, and only five separate areas, totaling about 31 km^2, supported population densities approaching 50% of those described by Grinnell (1932), Hawbecker (1951), Shaw (1934), and Williams (in press).

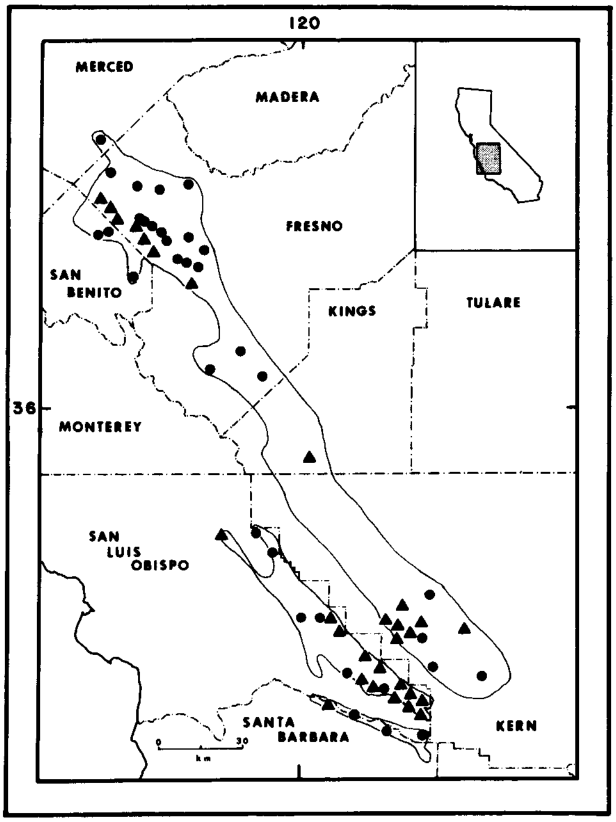

FIG. 3. Distribution of *Dipodomys ingens* in California. Triangles mark approximate locations of extant colonies; circles show locations of colonies, based on published records and specimens in museums, that are now extinct. The lines encircling locality symbols encompass the approximate historic distribution of giant kangaroo rats (Williams, in press).

FOSSIL RECORD. Fossils of *D. ingens* are known only from the McKittrick brea deposits in western Kern County, California (Kurtén and Anderson, 1980; Schultz, 1938). A radiocarbon date for plant material from the McKittrick deposits is 38,000 ± 2,500 years ago (Berger and Libby, 1966). Giant kangaroo rats are found in the same area today (Williams, in press).

FORM AND FUNCTION. The body hair of *D. ingens* is relatively thick, long, and silky. The dorsal guard hairs have a maximum length of 12–13 mm and a maximum width <45 μm. The shaft is almost uniform in diameter, tapering abruptly at the ends. Cortical granules extend 3–4 mm along the length of the shaft, and medullary aggregations are no more than four abreast. There is no prominent division of the medullary substance into cells (Mayer, 1952). The vibrissae are the most conspicuous tactile hairs, but others are located in the chin, foreleg, cheek, supraorbital, and heel regions (Eisenberg, 1963).

The dorsal skin gland consists of modified sebaceous glands and is scab-like in appearance. Size and activity of the gland in *Dipodomys* vary by species, sex, and season. Secretions of the gland function for communicating with other individuals (Quay, 1953). There are three pairs of mammary glands and nipples, one pectoral and two inguinal (Grinnell, 1932).

About 7% ($n = 29$) of a sample of *D. ingens* lacked interparietal bones, and in 69%, the interparietals consisted of one plate-like structure; small numbers of individuals had two, three, or four separate elements composing the interparietal complex. *D. ingens* was near the average (70.7%) of the combined sample of the 21 species of kangaroo rats examined for individuals exhibiting one plate-like bone, but had a greater than average number (3.3%) of individuals with no visible interparietals (Beer, 1965).

The muscular and skeletal structures of *D. ingens* do not differ markedly from those of nine other species of *Dipodomys* (Setzer, 1949) and *D. spectabilis*, the only species of kangaroo rat whose muscular system has been described in detail (Howell, 1932). Five skeletal indices vary considerably among *Dipodomys*, indicating varying degrees of specialization. *D. ingens* exhibits extreme specialization in the cranial index (breadth across bullae/length of skull; 66.2%), reflecting a greatly broadened skull compared to all other species except *D. deserti*. *D. ingens* has the second lowest crural index (lengths of tibia/femur; 130.6%), suggesting a relatively poor saltatorial ability. The tibioradial index (lengths of radius/tibia; 56.2%), however, is the second-most specialized, indicating greater than average elongation of the hind leg relative to the foreleg. Other skeletal indices of *D. ingens* are: humeroradial (lengths of radius/ humerus; 142.9%); intermembral (lengths of humerus + radius/ femur + tibia; 54.1%); femorotarsalmetatarsal (tarsometatarsus/ femur; 89.65%; Setzer, 1949).

Measurements (in mm) of the baculum of three individuals are: length, 10.8, 12.4, 13.1; height of base, 1.8, 2.0, 2.1; width, 1.6, 1.9, 1.9 (Burt, 1960). The base is relatively large; the shaft tapers gradually to its distal end, which curves abruptly downward. The base of the baculum is similar to *D. ornatus* in being rounded in cross section compared to the more oval bases of other kangaroo rat species (Lidicker, 1960*a*). Overall, the baculum of *D. ingens* is similar to *D. heermanni* (Burt, 1936, 1960) and *D. gravipes* (Best and Schnell, 1974).

The viscera of *D. ingens* are among the least specialized of nine species of kangaroo rats examined. *D. ingens* has a large caecum and little compaction of the visceral mass. The relatively large liver has nearly equal-sized and symmetrically-placed lobes. The right lobe of the liver extends to, and forms a capsule around, the anterior end of the kidney. The position of the right kidney relative to the left is markedly anterior in *D. ingens*. Several small and large patches of lymphoid tissue seen on the caecum of *D. agilis*, *D. deserti*, and *D. merriami* are absent in *D. ingens*, *D. heermanni*, *D. microps*, *D. nitratoides*, *D. ordii*, *D. panamintinus*, and *D. phillipsii*. The small intestine of *D. ingens* averages 274 mm in length, and the large intestine averages 430 mm in length. The ratio of the lengths of small to large intestines (63.7%) is greater for *D. ingens* than other species studied (Setzer, 1949).

Dipodomys ingens exhibits high hypothalamic and low peripheral thermosensitivities, suggesting that peripheral thermosensitivity plays a minor role in the regulation of body temperature. In unmanipulated animals, temperatures measured around the preoptic nuclei and hypothalamus increase with increasing ambient temperatures. Giant kangaroo rats respond to cooling of the preoptic nuclei and hypothalamus with an increase in oxygen consumption, huddling, and shivering. Heating of the preoptic nuclei and hypothalamus provoke a decrease in oxygen consumption to basal levels, accompanied by general quiescence. Unmanipulated animals sleep at ambient temperatures of 30°C; sleeping animals show a profound depression or elimination of preoptic nuclei and hypothalamus thermosensitivity (Glotzbach and Heller, 1975).

In unrestrained giant kangaroo rats during slow-wave sleep, in comparison to wakefulness, the threshold for metabolic heat production is lowered. Also lowered during slow-wave sleep is the proportionality constant relating rate of metabolic heat production to hypothalamic temperature. No increase in metabolic heat production occurs during paradoxical sleep when the hypothalamic temperature is lowered, indicating that the thermoregulatory system is inoperative in this phase of sleep. Metabolic rate during paradoxical sleep averages 0.088 cal g^{-1} min^{-1} (Glotzbach and Heller, 1976).

At ambient thermoneutrality (30°C), artificial cooling of the hypothalamus or skin results in decreases in total sleep time and the ratio of paradoxical sleep to total sleep time. In contrast, at low ambient temperatures total sleep time increases, but the ratio of paradoxical sleep to total sleep time does not. Low ambient temperatures result in a higher hypothalamic temperature and a differential inhibition of paradoxical sleep. Changes in the total duration of paradoxical sleep result mostly from changes in the frequency rather than duration of individual episodes of paradoxical sleep. Thus, the transition from slow-wave sleep to paradoxical sleep probably is partially dependent on the thermoregulatory conditions extant during slow-wave sleep (Sakaguchi et al., 1979).

ONTOGENY AND REPRODUCTION. The reproductive season may extend from January to May, based on capture of seven juveniles on 19–20 February, the largest of which weighed 103.5 g, and the capture of a female, pregnant with six fetuses, on 18 May. Three pregnant females taken in February each had five fetuses (Grinnell, 1932). A specimen in the Museum of Vertebrate Zoology, captured on 16 February, had 3 embryos, one of which was being reabsorbed (D. F. Williams, pers. comm.). During excavation of a burrow system on 3 March, a lactating female and four half-grown females were discovered; the adult had four placental scars (Shaw, 1934). The estimated mean litter size is 5.5 based on published counts of embryos (Jones, 1985). However, the number of fetuses carried until birth may be lower because some of the embryos may be reabsorbed (Grinnell, 1932). The mean value from all available counts of young, embryos, and placental scars is 4.6 ($n = 7$; D. F. Williams, pers. comm.). Four is probably the modal number of young born. There is no published information on numbers of litters per year. All six nipples of one nursing female showed use (Grinnell, 1932).

ECOLOGY AND BEHAVIOR. Areas inhabited by giant kangaroo rats generally receive <15 cm of precipitation annually, with nearly all falling between November and April. Pristine plant communities occupied by *D. ingens* probably were dominated by San Joaquin saltbush (*Atriplex polycarpa*) and perennial grasses such as *Stipa cernua*, *S. pulchra*, and *Poa scabrella* (Heady, 1977; Williams, in press). Since the introduction of weedy annual plants by Spanish missionaries, these communities have been dominated by annual plants. Summers within the range of *D. ingens* are hot, with daytime temperatures exceeding 38°C; winters are cool, with daytime temperatures rarely below about 10°C. Although the area inhabited by *D. ingens* is a climatic desert because of the long, hot season without rainfall, cool, wet winters promote production of annual grasses and forbs most years that averages near the midrange of production values reported for the Chihuahuan and Sonoran deserts (Williams, in press).

The habitat of *D. ingens* consists primarily of gently sloping piedmont plains, largely without shrub cover (Grinnell, 1932; Shaw, 1934; Williams, in press). Nearly all populations examined by Grinnell (1932) and Shaw (1934) were located on sandy loam soils, and both researchers stated that giant kangaroo rats were limited to shrubless areas with such soils. An inventory of extant colonies, however, showed that giant kangaroo rats lived on soils of widely varying textures, from fine sands to conglomerates of mixed pebbles and clay (Williams, in press). Nearly all extant colonies were located in suboptimal to marginal conditions, based upon comparisons with descriptions of habitat and densities of expansive colonies described earlier (Grinnell, 1932; Shaw, 1934), but no longer existing (Williams, in press). Williams (in press) noted that presence or absence of shrubs in areas inhabited by *D. ingens* seemed to be related to the texture of soils and intensity of livestock use, and that some colonies and individual burrows occurred in areas supporting many shrubs. Common plants in areas with colonies include: annual fescues (*Festuca megalura* and *F. microstachys*), Arabian grass (*Schismus arabicus*), bandergee (*Eastwoodia elegans*), California ephedra (*Ephedra californica*), cheesebush (*Hymenoclea salsola*), desert thorn (*Lycium andersonii*), fiddleneck (*Amsinckia douglasiana*), filaree (*Erodium cicutarium*), golden bush (*Haplopappus acradenius*), malpais blue grass (*P. scabrella*), peppergrass (*Lepidium nitidum*), red brome (*Bromus rubens*), San Joaquin saltbush, snakeweed (*Gutierrezia californica*), and winterfat (*Eurotia lanata*; Hawbecker, 1951; Shaw, 1934; Williams, in press).

Giant kangaroo rats have not been found in irrigated fields, but they reestablish colonies in fallow, dry-land grain fields when there are extant colonies on uncultivated ground nearby. Land continuously in dry-land cultivation does not support *D. ingens* (Williams, in press).

Wherever giant kangaroo rats were found by Grinnell (1932: 316), they dominated the community to the exclusion of other rodent species. He wrote, "Over thousands of acres the 'colonies' are spaced out over the level or rolling cattle-range, this being here apparently the only rodent, taking the place of the ground squirrels elsewhere." Hawbecker (1944, 1951) and Tappe (1941) corroborated some of these observations, finding that *D. ingens* excluded all other nocturnal rodents from areas where it occurred. Tappe (1941) found *D. ingens* to be dominant on gentle slopes; Hawbecker (1951) reported that slope was less a factor in the dominance of *D. ingens*

FIG. 4. Photograph of a precinct of *Dipodomys ingens* in an ungrazed, annual grassland community (*Atriplex* in the background) near Taft, Kern Co., California, in August 1979. Note that plants (mostly *Bromus rubens*) have been clipped close to the ground by the resident giant kangaroo rat.

than was lack of shrub cover, but reported that it did not occupy slopes steeper than about 9% (about 6°). Williams (in press) found colonies on slopes varying from 2 to 20°, although most colonies were on more level ground, generally with slopes <6°. Colonies of *D. ingens* where no other species of rodents occurred were not found by Williams (in press).

A population of *D. ingens* on the Carrizo Plain, San Luis Obispo Co., did not exclude other species of rodents to the extent reported by others (Braun, 1983). Six rodent species coexisted with *D. ingens*: *D. nitratoides*, *D. heermanni*, *Perognathus inornatus*, *Ammospermophilus nelsoni*, *Spermophilus beecheyi*, and *Onychomys torridus*. *D. ingens*, *D. nitratoides*, and *Perognathus inornatus* frequented the same trapping stations. Braun (1983) believed that lack of exclusivity supported the hypothesis that this population was living in suboptimal habitat.

Ammospermophilus nelsoni appropriates abandoned burrows of *D. ingens* (Hawbecker, 1944). Most burrows of *A. nelsoni* examined were constructed originally by *D. ingens* and *D. heermanni* (Hawbecker, 1947). *A. nelsoni* often is seen within giant kangaroo rat colonies, and frequently retreats into burrows indistinguishable from those occupied by *D. ingens*, giving the impression that members of the two species sometimes share the same burrow systems (Williams, in press).

Little direct evidence exists on aggression by giant kangaroo rats, but they seem to be much more aggressive than either *D. heermanni* or *D. nitratoides*, both of which are sympatric with *D. ingens*. An aggressive encounter between a giant kangaroo rat and a small mouse (probably *Peromyscus*) was reported by Shaw (1934), who speculated that exclusive occupancy of expanses of ground by giant kangaroo rats was maintained by interspecific aggression. A giant kangaroo rat was seen chasing an *A. nelsoni* out of a burrow (Hawbecker, 1944). A captive giant kangaroo rat, liberated into a room, quickly explored it before hopping boldly up to the observer, extending its body as high as it could reach on its hind legs and moving its head from side to side. Each time it was pushed away, it quickly returned to its original position (Williams, in press). This behavior is identical with the "investigatory upright" posture noted in captivity for *Dipodomys*, characterized as an aggressive or dominance stance (Eisenberg, 1963).

Predators include: barn owls (*Tyto alba*), great horned owls (*Bubo virginianus*), coyotes (*Canis latrans*), kit foxes (*Vulpes macrotis*), and badgers (*Taxidea taxus*; Grinnell, 1932; Hawbecker, 1943, 1944, 1945; Morrell, 1972). A weasel (*Mustela frenata*) was chased from a burrow system of either *D. ingens* or *A. nelsoni* (Hawbecker, 1944). Other common, nocturnal predators seen within colonies of giant kangaroo rats include prairie rattlesnakes (*Crotalis viridis*), gopher snakes (*Pituophis melanoleucus*), king snakes (*Lampropeltis getulus*), and coachwhips (*Masticophis flagellum*; Williams, in press).

Fleas (*Hoplopsyllus anomalus*), commonly associated with ground squirrels in western North America, and tick larvae (*Ixodes*) are found on *D. ingens* (Williams, in press). The cestode *Hymenolepis citelli* is the only recorded endoparasite of *D. ingens* (Simpson and Harmon, 1968).

Giant kangaroo rats often are found in areas heavily grazed, primarily by sheep and cattle (Grinnell, 1932; Shaw, 1934; Williams, in press). Livestock forage extensively on vegetation on the precincts of giant kangaroo rats (the precinct is the core of the territory of a giant kangaroo rat, located approximately over and encompassing an area somewhat larger than the burrow system), eating less of the vegetation between precincts. Both cattle and sheep clip the vegetation on precincts close to the ground (Hawbecker, 1944; Williams, in press). No adverse effects on giant kangaroo rats of grazing by cattle was noted by Braun (1983). The largest, densest, extant colonies are located in areas heavily grazed all year by cattle, but several colonies also are found in ungrazed areas. In the absence of grazers, the giant kangaroo rats clip the vegetation around their precincts, mowing an area averaging about 6 m in diameter (Fig. 4). They also clip plants along runways leading from one precinct to others (Williams, in press). These activities, and burrowing, seed caching, and dust bathing, turn and loosen the soil on the precinct, probably increasing porosity of the soil and percolation (Grinnell, 1932).

In spring, precincts show as distinct, evenly-spaced, dark green patches because of the more lush growth of herbaceous plants compared to intervening spaces. Plants on the precincts are the first to turn green after autumn rains and last to ripen and turn brown in spring (Grinnell, 1932). A comparison of productivity of *E. cicutarium* and *B. rubens* on precincts to that in the intervening spaces where the soils were hard packed revealed differences in height of vegetation (15.2 cm or more on precincts, 3.8 cm for the same plants in the intervening spaces). The amount of green biomass was 400.1 and 70.5 g in plots of 0.37 m^2 on and between precincts, respectively (Hawbecker, 1944).

Surfaces of typical precincts are roughly circular, show little or no mounding above surrounding terrain, and range from 1.8 to 7.7 m in diameter (Grinnell, 1932; Shaw, 1934; Williams, in press). Burrow systems have one to five separate burrow openings with three being typical. Although burrows with visible plugs can be found any time of the year, most burrow entrances lack visible plugs of earth (Williams, in press). Burrow openings are of two general types (Fig. 5): a vertical shaft with a circular opening with no apron of dirt near the mouth and no well-worn trail leading from the mouth; and a larger, more horizontally-opening shaft, usually wider than high and with a well-worn path leading from the mouth. Typically, a burrow system has two slanting tunnels and one vertical shaft opening to the surface. Average diameter of the vertical openings is 57–58 mm (range, 45–75; Grinnell, 1932; Williams, in press). Mean height and width of horizontal openings is 78–81 (range, 50–125) and 88–89 mm (range, 60–120), respectively (Grinnell, 1932; Williams, in press). Larger-than-typical openings probably have been altered by other animal species. Shape and orientation of entrances vary widely geographically (Williams, in press).

Burrows usually are dichotomous, with no reconnecting tunnels (Eisenberg, 1963; Grinnell, 1932). Tunnels typically are constructed in one layer, but one burrow was found with a three-layer arrangement of tunnels (Tappe, 1941). Measurements based on excavated burrow systems are: internal tunnel diameter, 50–75 mm, with occasional enlargements up to 150 mm; average tunnel depth, 263 mm with greatest depth of 463 mm; greatest tunnel length, 3 m. Total lengths of three systems, including side branches, measure 9.1, 7.3, and 8.2 m (Grinnell, 1932). Soil excavated from burrows has numerous seed hulls and other plant debris mixed in, suggesting that tunnels have been worked and reworked, perhaps over several years (Grinnell, 1932; Shaw, 1934). One nest located 330 mm below the surface consisted of sheep's wool, fine, shredded grass stems, and 0.5 l of seed hulls (Grinnell, 1932).

Rain water in areas inhabited by giant kangaroo rats usually penetrates the soil only to a depth of 220–230 mm, leaving most of the burrows relatively dry. The scanty rainfall and consistency of fine sandy loam soils inhabited by *D. ingens* are thought to be factors in determining distribution of this species (Grinnell, 1932).

Burrow construction and maintenance involve digging movements consisting of rapid, alternate forward and back motions of the forelimbs until a pile of earth accumulates under the animal. Then, the hind legs are brought forward to kick the pile to the rear. When a pile accumulates behind the animal, it turns and pushes the dirt to the entrance with its hands and chest. Giant kangaroo rats push and pat the soil of the burrow walls to compact it. Cracks and caveins in the tunnels are pushed and patted until the soil is firm (Eisenberg, 1963).

Giant kangaroo rats store seeds in parts of their burrows, but apparently not in small pits in the walls of their tunnels as do most other kangaroo rat species (Eisenberg, 1963; Shaw, 1934). Seeds are not always stored directly after collection. Giant kangaroo rats cut the ripening heads of grasses and forbs and cure them in small surface pits located on the precinct (Shaw, 1934). Surface pits examined by Shaw (1934) were uniform in diameter and depth (about 2.5 cm), placed vertically in firm soil, and filled with seed pods. After placing seeds and seed heads in pits, the animal covered them with a layer of loose, dry dirt. Sets of pits associated with one precinct covered 0.8, 2.6, 3.2, 5.1, 6.1, and 7.3 m^2. The 5.1-m^2 cache consisted of 875 separate pits. Shaw (1934) surmised that pits were filled with the contents of the cheek pouches after one trip to harvest seeds and that before being moved underground the seeds were sun-dried to prevent molding. A similar behavior in some populations of *D. ingens* involves making large stacks of separated seed heads on the surface of precincts (Hawbecker, 1944; Williams, in press). The material is cured, then stored underground. Stacks measured by Hawbecker (1944) averaged about 10 by 10 by 61 cm, although one measured 1.2 by 1.8 m and was 10 cm deep; each stack appeared to belong to one giant kangaroo rat.

Large caches of seeds are stored underground. In one den, 24 caches were found; 12 apparently were old, filled mostly with sand and empty seed pods, and 12 others were newer, consisting primarily of seeds of *Erodium* and *Lepidium*. Measurements (means in cm) of the newer caches were: depth below ground 14; length, width, and height 26, 14, and 10, respectively. In another den, nine caches were located, each containing 1.1–9.1 l of seeds (Shaw, 1934).

Giant kangaroo rats are primarily granivorous. Of 875 surface pits on one precinct, numbers of pits filled with each type of seed head or pod were: *L. nitidum*, 873; *Oenothera*, 179; *Erodium*, 169; *Gnaphalium*, 5; *Plantago*, 4; *Atriplex*, 4; and *B. rubens*, 1 (Shaw, 1934). When available, they also eat some green, herbaceous plants. There is no evidence, however, that they eat mostly green vegetation, despite a statement to this effect by Burt and Grossenheider (1976). Grinnell (1932:313) examined three nursing females who had their cheek pouches "literally crammed with green stuff" and speculated that green foliage might provide essential nutrients during lactation. Other individuals, including a young female and adult males, were captured with foliage and fruits of *Lepidium* and foliage of *Erodium* in their cheek pouches (Grinnell, 1932). A live hymenopteran insect was found in the cheek pouch of a giant kangaroo rat and abdomens of three ants and wings of another were found in different pit caches (Shaw, 1934). A giant kangaroo rat was kept in captivity on a diet that included seeds, lettuce, and mealworm larvae (*Tenebrio*). Mealworms were caught with the forepaws, but before picking one up, the animal pushed and patted at it with its forepaws for a few seconds, then grasped it and bit off an end, usually the head. In captivity, giant kangaroo rats were maintained for periods of from 2 weeks to >2 years on a diet of air-dried seeds, consisting primarily of millet, oat, and sunflower. When provided, captive individuals ate more green forbs than annual grasses, and usually ignored blades of perennial grasses.

Fecal pellets are about 7 mm long by 2.5 mm in diameter. Accumulations of fecal pellets are not found within burrows, but individual pellets and small piles are common on dust aprons outside entrances and on trails between burrows (Grinnell, 1932). In captivity, animals do not eliminate wastes in their nest; feces are voided anywhere within the cage, but urine typically is deposited in one corner. Often, the spot is covered by kicking sand over it with the hind feet (Eisenberg, 1963).

Sand bathing, scent marking, and urination influences the behavior of other individuals. Sand or dust bathing behavior in *D. ingens* involves three distinct components: a rapid dig with the hands, followed by either side- or belly-rubs. The side-rub involves lowering the cheek to the substrate and extending the body in a forward glide, followed by alternate flexing and extending of the body while the animal lays on its side. The belly-rub consists of extension and flexion of the body while the animal lays with its ventral parts pressed against the substrate. Scent marking or perineal drag is often combined with the terminal portion of the belly-rub during dust bathing. The perineal region is pressed to the substrate while the animal slowly moves forward (Eisenberg, 1963). Local disturbances to soil caused by cattle often are used as dust-bathing areas by giant kangaroo rats (Braun, 1983).

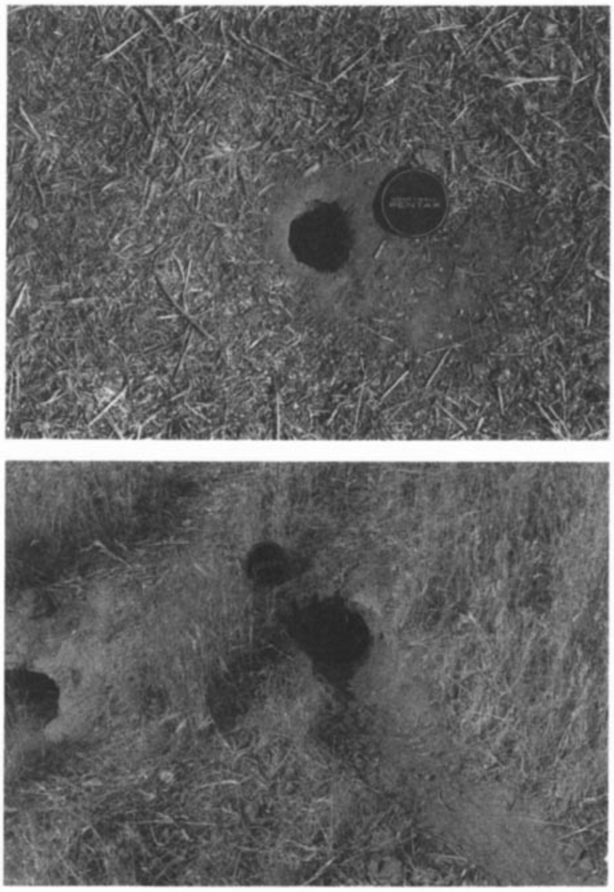

FIG. 5. Photographs of typical openings to burrows of *Dipodomys ingens*; above, circular opening to vertical shaft; below, opening to sloping tunnel.

Giant kangaroo rats assume a curled posture when sleeping. The head is tucked under the body so the animal rests partly on the anterior-dorsal surface of the head and on its hind feet (Glotzbach and Heller, 1975). The tail usually is curled around the body when in this posture. When warm, an animal often lays stretched out with its ventral side and chin resting on the ground (Eisenberg, 1963).

Dipodomys ingens uses a shuffle or bipedal walk while foraging. Quadrupedal and bipedal ricochets or hops are used for more rapid travel. The quadrupedal hop involves an alternation of forelimbs and hind limbs in striking the ground simultaneously. In bipedal saltation, the hind limbs strike the ground simultaneously (Eisenberg, 1963). High speed travel is estimated to be >3 m/s (Braun, 1985).

Vocalizations of *D. ingens* apparently are similar to most other members of the family Heteromyidae. A scratchy growl of low pitch generally is given when an animal is harassed by another or when its nest is defended. An animal under attack blends the growl with a whining squeal of greater pitch and intensity. This sound also is made when an animal is injured. A low intensity grunt generally is given by a frightened animal. When excited, a low chuckling sound is given (Eisenberg, 1963).

Drumming with the hind feet occurs in captive giant kangaroo rats when they are aroused. Drumming generally occurs after an encounter with an intruder and after taking refuge in its burrow or in a neutral corner of a cage (Eisenberg, 1963). Giant kangaroo rats foot drum in the wild while within their burrow system (Shaw, 1934). Shaw (1934:278) noted ". . . in the summer when their granaries are full, the animals may be induced to reply to one's beating with the hand upon the ground above them . . . ."

Giant kangaroo rats equipped with blinking light-emitting diodes emerged from their burrows soon after sunset and mean time from first emergence to last disappearance was about 1.8 h. There was no second period of activity before dawn. Animals were seen above ground only for an average of 15.2 min/night during the 1.8-h period. Time spent above ground (foraging bouts) lasted about 80.7 s; animals performed 3.5 bouts/h. They spent most of their time above ground near their precincts; individuals averaged using 2.2 grid squares (5 by 5 m) per bout, with a maximum distance travelled of 47.1 m by one individual during one bout. During bouts, animals moved slowly, spending an average of 47.5 s in each square. Activity patterns appeared to be unaffected by distance from the home burrow, weather (snow, rain, wind), moonlight, or season (Braun, 1983).

Home range sizes range from 60 to 350 m^2 ($\bar{X} = 239.3\ m^2$), using the 95% contour interval of three-dimensional utilization distributions, based upon both trap captures and direct observations (Braun, 1983, 1985). There are no significant differences in sizes of home ranges of males and females. Paradoxically, the average size of the home ranges of giant kangaroo rats is much smaller (0.04 ha) than those of smaller-sized species of *Dipodomys* and about one-half the extent of other large-sized species. Home range sizes for other kangaroo rats range from 1.65 ha (*D. merriami*) to 0.072 ha (*D. spectabilis*; Braun, 1985).

Independent observations and time-weighted measures gave slightly different centers of activity close to the burrow system, indicating that the precinct is the most intensely used location in the home range (Braun, 1985). Giant kangaroo rats are territorial, exhibiting regularly-spaced precincts and living singly in their burrow systems. Individual burrow systems rarely or never permanently contain more than one adult (Grinnell, 1932; Shaw, 1934). Of five excavated burrows in which cyanide canisters had been previously placed, one was occupied by a male-female pair of adults and others were vacant or occupied by no more than one adult (Shaw, 1934). By measuring overlap between home ranges of individual animals, Braun (1985) showed that individuals exhibited strict intrasexual avoidance, with moderate levels of intersexual contact. Although each individual had a distinct burrow system, animals frequently entered burrows beyond their home precincts during nightly periods of activity.

Estimates of density, based on counts of precincts, ranged from 18 to 69/ha in the larger and denser colonies (Grinnell, 1932; Williams, in press). Grinnell (1932) calculated a mean of 52/ha, but noted that the value was too high for the low point in the annual cycle of density and too low for the maximum. A mean density of 22 active burrow systems/ha was found in August in four of the largest extant colonies in 1979. Other colonies of giant kangaroo rats were smaller and less dense; the largest covered about 125 ha, but most consisted of from 5 to 50 precincts, each isolated by several hundred meters or more from other colonies (Williams, in press). Braun (1985), employing both trapping and counts of burrows, estimated a density of 25 adults/ha on her study site. Although this colony was typical in density for the larger colonies extant, she interpreted her findings as indicating that this colony was not living in prime habitat.

Because of the decline in numbers of giant kangaroo rats and the continuing threats to remaining colonies, the California Fish and Game Commission designated *D. ingens* as a state Endangered Species in 1980 (Williams, in press). In 1987, the United States Fish and Wildlife Service added *D. ingens* to the federal List of Endangered and Threatened Wildlife (United States Department of the Interior, 1987).

GENETICS. *Dipodomys ingens* has a diploid number of 64 chromosomes with a fundamental number of 98. The autosome pairs include 4 metacentrics, 14 submetacentrics, and 13 acrocentrics. The structure of the X chromosome is submetacentric and the Y is acrocentric. The chromosomes are most similar in structure to *D. panamintinus* and *D. heermanni*. According to Stock (1974), this *heermanni* subgroup arose in the early Pleistocene and had an ancestral karyotype of $2n = 70$. *D. ingens* shared a common ancestor with *D. heermanni* in the late Pleistocene, diverging from *D. heermanni* only after fixation of the present karyotype of *D. heermanni*. The chromosomes of *D. ingens* diverged in structure by a process that reduced the number of acrocentric autosomes by two pairs, concomitantly increasing the number of submetacentric autosomes by two pairs from the condition in *D. heermanni*. Pericentric inversions in two pairs of acrocentrics, or other mechanisms increasing the autosome arms in the karyotype by four, were responsible.

Major interspecific variation in the proportions of highly reiterated sequences of satellite DNA are found in the genomes of 22 species of *Dipodomys* (Hatch et al., 1976). *D. ingens* clusters with a middle group of three, based on chromosome numbers, total nuclear DNA and amount of satellite DNA, and the ratio of heavy satellite DNA to intermediate-density DNA. The proportions of liver DNA in neutral cesium chloride gradients for *D. ingens* are: principal, 46%; intermediate, 23%; satellite, 16% intermediate-density DNA (density of 1.707 g ml^{-1}) and 15% heavy satellite DNA (density of 1.713 g ml^{-1}). These values are similar to those of *D. heermanni*, *D. panamintinus*, and *D. stephensi* (Mazrimas and Hatch, 1972).

REMARKS. Grinnell (1922) allied *D. ingens* with *D. heermanni*, *D. stephensi*, and *D. panamintinus* in the *heermanni* species group. Based on bacular structure, Burt (1936, 1960) placed *D. ordii* with *D. ingens* in the *heermanni* group. Lidicker (1960*a*) and Best and Schnell (1974) drew a close relationship between *D. ornatus* and *D. ingens* based on structure of bacula. A distance phenogram of bacular measurements most closely linked *D. ingens* with *D. gravipes* (Schnell et al., 1978). Setzer (1949), based on skeletal and visceral adaptations, placed *D. ingens*, *D. heermanni*, *D. agilis*, *D. venustus*, and *D. elephantinus* together in his *heermanni* group. Lidicker (1960*b*), considering a variety of evidence presented by previous researchers, realigned the species associated with *D. ingens*, placing it in a *heermanni* subgroup that included *D. heermanni*, *D. panamintinus*, *D. stephensi*, and *D. gravipes*. The *heermanni* group of Stock (1974) consisted of five distinct subgroups based on karyotypes: A, *D. gravipes* and *D. stephensi*; B, *D. heermanni*, *D. panamintinus*, and *D. ingens*; C, *D. deserti*; D, *D. agilis*, *D. elephantinus*, *D. peninsularis*, and *D. venustus*; E, *D. microps*. Phenograms based on skeletal measurements by Schnell et al. (1978) linked *D. ingens* most closely with *D. spectabilis* using average distance coefficients, and with *D. gravipes* using correlation coefficients. Subsequent phenetic analyses by Best (in press) based on 19 external and skull measurements linked *D. ingens* most closely with other large-sized kangaroo rats, *D. spectabilis* and *D. deserti*, when groupings were based on distance coefficients, but with *D. gravipes* and *D. stephensi* (males) or with *D. panamintinus* (females) when correlation coefficients were used.

The name *Dipodomys* means two-footed mouse. The specific epithet, *ingens*, is Greek for giant.

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Editors of this account were B. J. Verts, Troy L. Best, and J. Knox Jones, Jr. Managing editor was Don E. Wilson.

D. F. Williams, Department of Biological Sciences, California State University, Stanislaus, Turlock, California 95380; and K. S. Kilburn, Department of Biology, West Virginia State College, Institute, West Virginia 25112.