Dipodomys nitratoides.   By Troy L. Best

Dipodomys Gray, 1841

Dipodomys Gray, 1841:521. Type species *Dipodomys phillipsii* Gray, 1841, by original designation.
Perodipus Fitzinger, 1867:126. Type species *Dipodomys agilis* Gambel, 1848.
Dipodops Merriam, 1890:71. Type species *Dipodomys agilis* Gambel, 1848.

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae. The genus *Dipodomys* contains 22 species that have been divided into groups on the basis of internal, external, and bacular morphology, chromosomal configurations, and protein variation (for example, Best and Schnell, 1974; Grinnell, 1921; Hamilton et al., 1987; Johnson and Selander, 1971; Lidicker, 1960a; Schnell et al., 1978; Setzer, 1949; Stock, 1974). A key to the species of *Dipodomys* as modified from Hall (1981) and Williams and Genoways (in press) follows:

1 Four toes on each hind foot 2
  Five toes on each hind foot (fifth is half-way up inside of foot and little more than the claw is exposed) 11
2 Occurring in northern Texas and southwestern Oklahoma .... *D. elator*
  Not occurring in northern Texas and southwestern Oklahoma 3
3 Occurring in southern Oregon and northern California north of a line from Suisun Bay to Lake Tahoe ...... *D. californicus*
  Occurring in California south of the mentioned line as well as in the states east of California; also in Mexico 4
4 Length of hind foot <42 mm 5
  Length of hind foot >42 mm 9
5 Interorbital breadth >50% of basal length of cranium; tail-tip dusky or blackish brown 6
  Interorbital breadth <50% of basal length of cranium; tail-tip pure white following an all black segment, or rarely, instead, distal 25% or more of tail all jet black .... *D. phillipsii*
6 Occurring in San Joaquin Valley of California, or on Margarita or San José islands of Baja California 7
  Not occurring in San Joaquin Valley of California, or on Margarita or San José islands of Baja California .... *D. merriami*
7 Occurring in San Joaquin Valley of California .. *D. nitratoides*
  Not occurring in San Joaquin Valley of California 8
8 Occurring on Margarita Island, Baja California .... *D. margaritae*
  Occurring on San José Island, Baja California ...... *D. insularis*
9 Upper parts pale ochraceous buff; ventral dark tail-stripe absent, or pale if present; no black band in front of white tip of tail; length of hind foot 50–58 mm .... *D. deserti*
  Upper parts brownish; ventral tail-stripe well defined; tail with subterminal blackish band and tipped with white; length of hind foot 45–51 mm 10
10 White tip of tail <25 mm, or absent altogether ...... *D. nelsoni*
   White tip of tail >25 mm .... *D. spectabilis*
11 Length of head and body usually <130 mm; greatest width across maxillary roots of zygomatic arches <25.5 12
   Length of head and body usually >130 mm; greatest width across maxillary roots of zygomatic arches >25.5 mm .... *D. ingens*
12 Occurring east of Sierra Nevada-Tehachapi-Southern Coast Range mountains 13
   Occurring west of Sierra Nevada-Tehachapi-Southern Coast Range mountains 16
13 Lower incisors awl-like (anterior faces rounded) 14
   Lower incisors chisel-like (anterior faces flat) .... *D. microps*

14 Total length usually <280 mm 15
   Total length usually >280 mm 16
15 Tail long and crested; ventral tail stripe dark and unbroken to end of tail; interparietal acutely pointed posteriorly and triangular; diploid number of 72 chromosomes .... *D. ordii*
   Tail short and not crested; ventral tail stripe pale and does not extend to end of tail; interparietal rectangular to oval; diploid number of 74 chromosomes; occurs only in southern Texas and adjacent Mexico .... *D. compactus*
16 Length of hind foot usually <42.5 mm; San Jacinto Valley and vicinity (western Riverside, northern San Diego, and southern San Bernardino counties, California) ... *D. stephensi*
   Length of hind foot usually >42.5 mm; north of San Jacinto Valley, but wholly within California and western Nevada .... *D. panamintinus*
17 Posteroexternal angle of maxillary root of zygomatic arch prominent and sharp; width across maxillary roots of zygomatic arches >54.8% of greatest length of cranium 18
   Posteroexternal angle of maxillary root of zygomatic arch weakly angled; width across maxillary roots of zygomatic arches <54.8% of greatest length of cranium 19
18 Occurring in California .... *D. heermanni*
   Occurring in Baja California .... *D. gravipes*
19 Width of maxillary arch at middle averaging >5 mm; pinna of ear averaging 15.5 or more from crown 20
   Width of maxillary arch at middle averaging <5 mm; pinna of ear averaging 15.4 or less from crown 21
20 Color of upper parts close to cinnamon buff; ear mostly brownish; dark ventral tail-stripe half-way toward end narrower than lateral white stripe; pinna of ear averaging >16.7 mm from crown .... *D. elephantinus*
   Color of upper parts pale cinnamon brown to deep cinnamon brown; ear mostly blackish; dark ventral tail-stripe half-way toward end wider than lateral white stripe; pinna of ear averaging <16.7 mm from crown .... *D. venustus*
21 Occurring principally north of Los Angeles Basin in California; greatest length of cranium usually >39.4 mm .... *D. agilis*
   Occurring principally in and to the south of Los Angeles Basin; greatest length of cranium usually <39.3 mm .... *D. simulans*

Dipodomys nitratoides Merriam, 1894

San Joaquin Kangaroo Rat

Dipodomys merriami nitratoides Merriam, 1894:112. Type locality "Tipton, San Joaquin Valley [Tulare Co.], California."
Dipodomys nitratoides: Grinnell, 1921:96. First use of current name combination.

CONTEXT AND CONTENT. Context noted in generic summary above. Three subspecies of *D. nitratoides* are recognized (Hall, 1981):

D. n. brevinasus Grinnell, 1920:179. Type locality "Hayes Station, near B. M. 503, 19 miles southwest of Mendota, Fresno County, California."
D. n. exilis Merriam, 1894:113. Type locality "Fresno, San Joaquin Valley [Fresno Co.], California."
D. n. nitratoides Merriam, 1894:112, see above.

DIAGNOSIS. Several congeners occur sympatrically or near the range of *D. nitratoides*. *D. merriami* is not sympatric, but is similar morphologically (Hall, 1981). The dark dorsal and ventral

FIG. 1. *Dipodomys nitratoides* from near Buttonwillow, Kern Co., California.

tail stripes in *D. nitratoides* are broader than the white lateral tail stripes; conversely, in *D. merriami* the white lateral tail stripes are always broader than even the dark dorsal one, and the dark ventral one is narrower or almost lacking (Grinnell, 1922). The baculum of *D. nitratoides* is much longer (13.3 mm) than that of *D. merriami* (10.8 mm), and is among the longest in the genus (Best and Schnell, 1974). *D. ingens, D. panamintinus, D. heermanni,* and *D. microps* have five toes on the hind foot instead of four as in *D. nitratoides*; they also are much larger (Hall, 1981).

GENERAL CHARACTERS. *Dipodomys nitratoides* (Fig. 1) is one of the smallest members of the genus (Best, in press). The upper parts are uniform fulvous or clay color, darkened with sepia from the abundant admixture of black-tipped hairs, and darkest on the head. Facial crescents are dusky and meet over the bridge of the nose. The upper and lower tail stripes are sooty blackish, meeting along the terminal one-third, thus interrupting the white side stripes. The dorsal tail stripe is darker than the back and the crested part of the tail is the same color as the back. The ventral tail stripe is dull fulvous, continuous to the end of the tail. The inner aspect of hind legs to heel are dull fulvous, and the under parts of the thigh stripe are white. The posterior aspect of the ankles and lower leg is black. The sides and flanks are tinged with ochraceous-buff. There are black crescents at the base of the whiskers that are sharply defined and meet in a median line, so that the bridge of the nose is black. The superciliary stripe is whitish and not interrupted. The under parts are silky white. The spot over the eye is obscured by dark-tipped hairs (Merriam, 1894). There is little difference in pelage shade between juveniles and adults. However, there is a difference in texture of the coat; juvenile pelage is finer than that of adults (Hoffmann, 1975).

Morphologically, *D. nitratoides* is adapted for ricochetal locomotion (Eisenberg, 1963), and its skull is similar to that of other *Dipodomys* (Fig. 2). The hind foot is 37% and the tail is 148% of the length of head and body (Hatt, 1932). Mean measurements (in mm) of 276 adult males and 200 adult females, respectively, from throughout the range of the species are: total length, 240.0, 235.1; length of body, 97.1, 98.1; length of tail, 140.7, 137.0; length of hind foot, 35.3, 34.9; length of ear, 12.1, 11.9; basal length of cranium, 18.8, 18.6; greatest length of cranium, 34.4, 34.0; maxillary arch spread, 18.8, 18.7; interorbital width, 10.7, 10.6; nasal length, 12.3, 12.2; intermaxillary width, 6.8, 6.8; alveolar length, 4.5, 4.4; lacrimal length, 3.1, 3.1; maxillary arch width, 4.7, 4.7; basioccipital length, 5.2, 5.1; greatest depth of cranium, 11.7; 11.5; greatest width of cranium, 22.4, 22.1; zygomatic width, 16.1, 16.0; and nasal width, 3.1, 3.0 (Best, in press). Average mass is 43.9 g (range, 39.6–52.6; Grinnell, 1922).

Of 19 morphologic characters, 12 exhibit significant sexual dimorphism in size. Males are significantly larger than females; these characters include total length, length of tail, length of hind foot, basal length of cranium, greatest length of cranium, maxillary arch spread, greatest depth of cranium, and greatest width of cranium (Best, in press).

There is geographic variation in most external and cranial characters among populations of *D. nitratoides* (Hoffmann, 1975). Average measurements (in mm) for *D. n. nitratoides, D. n. exilis,*
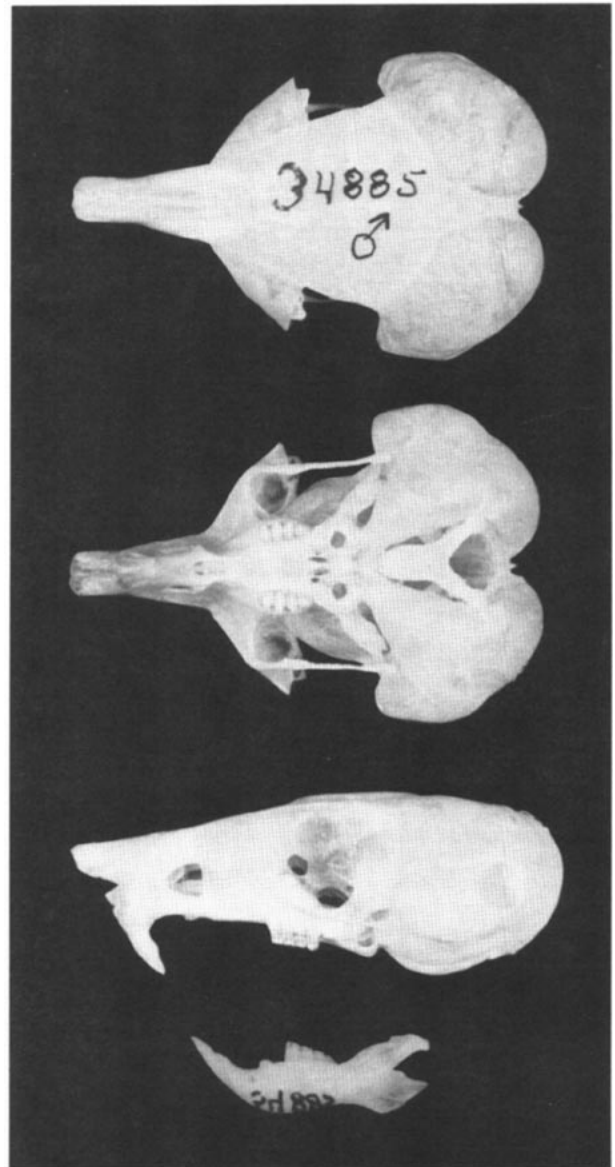

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Dipodomys nitratoides* (male from Kern County, California, Museum of Southwestern Biology 34885). Greatest length of cranium is 35.3 mm. Photographs by J. L. Dobie and T. L. Best.

and *D. n. brevinasus,* respectively, are: length of tail, 137.7, 137.4, 148.8; length of hind foot, 34.0, 33.4, 36.0; width of bulla, 21.6, 21.7, 22.6; condylobasal length, 29.9, 29.7, 31.4. Percent of red pigment for the three subspecies are 15.8, 16.2, and 17.7, respectively (Boolootian, 1954).

DISTRIBUTION. *Dipodomys nitratoides* occurs only in the San Joaquin and adjacent valleys of California (Fig. 3; Hall, 1981). The altitudinal range is from about 50 to 800 m (Grinnell, 1933; D. F. Williams, pers. comm.).

FOSSIL RECORD. The fossil record of the Dipodomyinae (*Prodipodomys, Etadonomys, Dipodomys*) extends back to the Pliocene in western North America. *Prodipodomys,* a Blancan and Irvingtonian genus, was formerly thought to be ancestral to *Dipodomys.* It has rooted cheekteeth. *P. centralis* is thought to be a generalized form that persisted after the development of the more advanced *P. idahoensis.* Instead of being directly ancestral to *Dipodomys, Prodipodomys* was probably a collateral lineage (Kurtén and Anderson, 1980).

No fossils of *D. nitratoides* are known. However, during mountain building in the Quaternary, kangaroo rats that had reached

central California from the parental center (northern tableland of Mexico and adjoining southeastern California and southwestern Nevada) became isolated by the emergence of the Tehachapi Mountains. This mountain range separated the California animals from populations farther south and east, allowing *D. nitratoides* to differentiate from *D. merriami* (Setzer, 1949).

FORM AND FUNCTION. San Joaquin kangaroo rats are independent, or nearly so, of exogenous water (Kenagy, 1973); they can live on metabolic water (Eisenberg, 1967*b*.) Sebaceous and mucous glands are present at the oral lips and angle (Quay, 1965). The percentage of alpha cells (1,000 chromophil cells counted/animal) in pancreatic islets is 22.5 (Quay, 1960).

As in other *Dipodomys*, *D. nitratoides* moves by bipedal locomotion (Eisenberg, 1967*b*.) Skeletal indices include: humeroradial, 155.0; intermembral, 54.1; crural, 137.4; tibioradial, 57.0; femoratarsal-metatarsal, 98.3; and cranial, 65.5. *D. nitratoides* has an average specialization (based upon skeletal and visceral measurements) of 8.5 on a scale of 1–11; it is one of the most specialized species in the genus (Setzer, 1949).

The dorsal guard hairs have a maximum width <56 μ, a maximum length of 15 mm, and a medullary width up to 45 μ (Mayer, 1952). Adults molt throughout the year. However, most molt from July through October. The new coat can be distinguished in molting individuals by its darker color. Just before molting, the fur is faded and reddish in hue (Hoffmann, 1975).

The interparietal is composed of a variable number of bones; there is one bone present in 87.8%, two bones in 6.1%, three bones in 4.0%, and no interparietal in 2.0% of *D. nitratoides* (Beer, 1965). The interparietal averages 1.58 mm in width (Wood, 1935).

The evergrowing molariform teeth are closed at the base in adults (Nader, 1966). All teeth erupt at nearly the same time so that the crown patterns of the whole series can be seen in the same animal. The enamel develops small breaks after a considerable period of wear. The third molars are subtriangular. The other cheekteeth are much compressed antero-posteriorly. The anterior surface of the lower incisor is rounded. The masseteric ridge of the mandible is small, and slopes steeply upward. The symphysis ends at the level of the mental foramen (Wood, 1935).

The auditory ossicles are small, as are the intra-aural muscles associated with them. The oval window opens into the scala vestibuli much higher up in the cochlear spiral than in other mammals. The stapes is secured in the oval window by two sheaths of connective tissue. The general form of the cochlea is a truncated cone, except that the cochlea is markedly opened out at the base. The number of half-turns seen in horizontal section varies between seven and eight. Body mass does not bear any relationship to the size of the cochlea. The basilar membrane supports the organ of Corti and the associated supporting cells. The dimensions of this membrane may play a major part in frequency analysis of sound; width starts at about 200 μ, increases to 300 μ in the subapical turn, and then decreases slightly at the apex. The cells of Hensen increase in size toward the apex of the cochlea and the cells of Claudius decrease in size from the base to the apex (Pye, 1965).

This species has the most highly developed glans penis of all the *Dipodomys* in California. It is similar to that of *D. merriami*, except for the extremely elongated bacular projection that makes up almost 50% of the total length of the glans. Only the main body contains spines. The urethral lappets are like those of *D. merriami*, except the margins of the lobes are cleft deeper and a rod of tissue with a greater opacity is in the center of each lobe. The curvature of the tip is 142° (Kelly, 1969).

The baculum of *D. nitratoides* is similar to that of *D. merriami*, but there is no overlap in measurements of length between these species (Burt, 1960). Mean measurements (in mm) are: length, 13.34; height of base, 1.13; and width of base, 0.93 (Best and Schnell, 1974). The baculum has a nearly round base (dorso-ventral/lateral diameter of base) of 1.23, an index of robustness (dorso-ventral diameter of base + lateral diameter of base × 100/length) of 15.3, and a relative length (body length/baculum length) of 7.62 (Lidicker, 1960*b*). Generally in *Dipodomys*, there is a significant relationship between bacular and body length. However, this is not true in *D. nitratoides*, which has a long baculum in comparison with its small body size (Best, 1981).

ONTOGENY AND REPRODUCTION. *Dipodomys nitratoides* has been bred in the laboratory in cages 150 by 210 cm, 196 by 199 cm, and in a cage having a floor area of 0.56 m² (Eisenberg, 1967*a*). In the wild, the breeding season in December
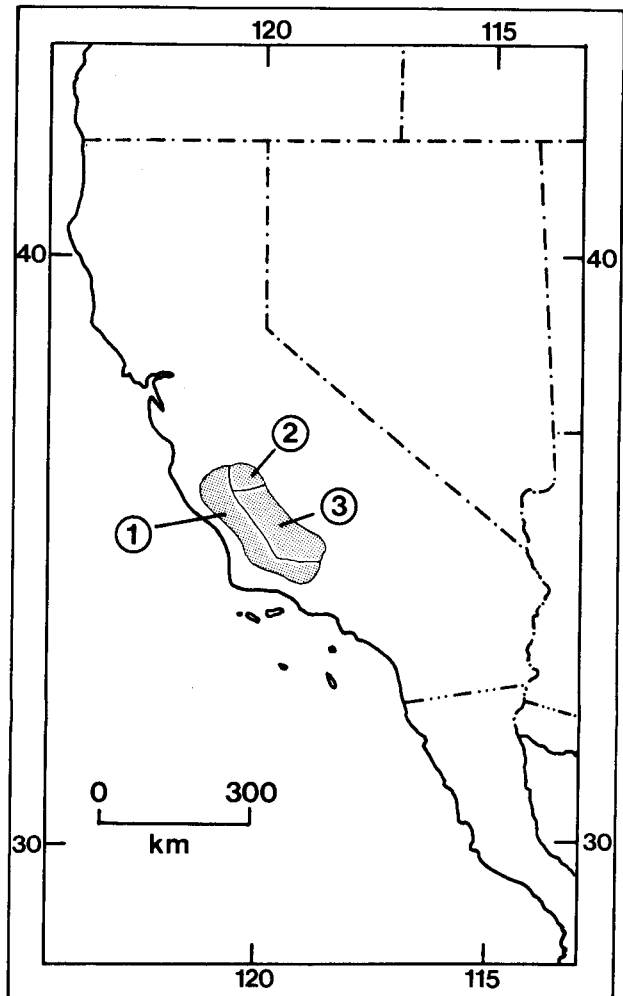

FIG. 3. Distribution of *Dipodomys nitratoides* in western North America (Hall, 1981): 1, *D. n. brevinasus*; 2, *D. n. exilis*; 3, *D. n. nitratoides*.

to August (Eisenberg, 1963) or throughout the year (Jameson and Peeters, 1988). Females may show post-partum estrus with conception taking place (Eisenberg, 1967*a*). The gestation period is 32 days (Eisenberg and Isaac, 1963), average litter size is 2.3 (with a mode of 2), average mass at birth is 4.0 g (Eisenberg, 1963), and average litter mass is 7.6 g (Jones, 1985).

The young are well developed at birth, except for the teeth. Lower incisors appear at 4 days and upper incisors appear at 7 days (Eisenberg, 1963). Body measurements (in mm) at birth, 10 days, 17 days, 33 days, and 40 days, respectively, are: length of body, 30, 40, 57, 75, 76; length of tail, 10, 32, 58, 110, 117; length of hind foot, 10, 18, 27, 32, 32.5; mass (in g), 2.5, 5.0, 9.0, 16.9, 19.1 (Culbertson, 1946). Adult mass is attained in 2.5–3 months (Eisenberg, 1963).

Eyes open at 10–11 days, auditory meatus opens at 8–9 days, dorsal pelage is complete in 6–7 days, and ventral pelage is complete in 9–10 days of age. The toes tend to be separate at birth; the cheek pouches, if present at all, are slight indentations on the lower side of the jaw that rapidly indent to become functional at about 2–3 weeks of age. The maturation of motor patterns follows an anterior to posterior gradient and the maternal retrieving responses begin to wane at the time of weaning (Eisenberg and Isaac, 1963).

At birth the mysticial, submental, ulnar-carpal, genal, and supraorbital hairs are present, and the eyes and auditory meatus are closed; the meatus opens (8–9 days) slightly before the eyes (10–11 days). Young may be able to perceive temperature changes, since cooling induces a specific vocalization. The young produce sounds of four types: faint peeping that accompanies grooming by the female; the "tic" sound accompanying sucking movements when the animal is off the teat; the low-scratchy whine when the animal
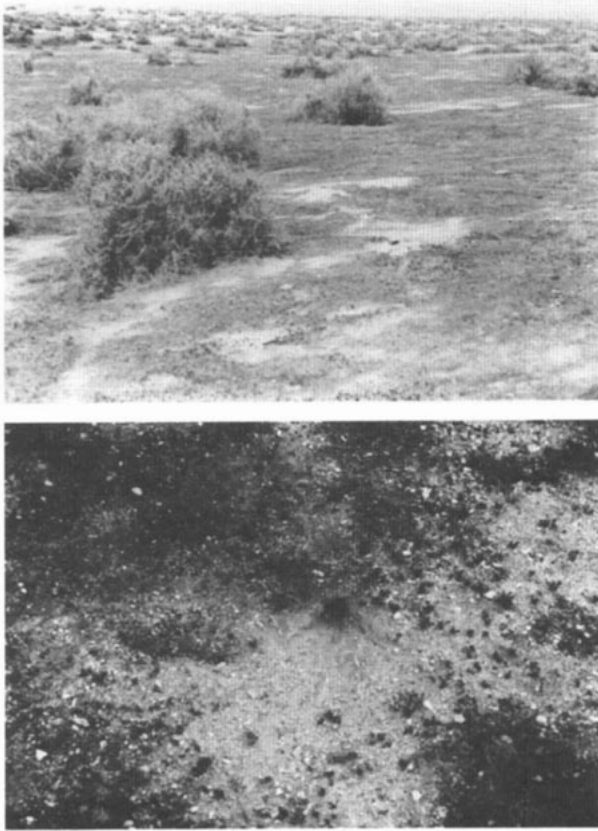
FIG. 4. Habitat occupied by *Dipodomys nitratoides* (above) and burrow entrance (below) near Buttonwillow, Kern Co., California.

is cold or isolated from the litter and the female; and a sharp squeal produced when the young are roughly handled. Dorsal pelage is dark brown by 6–7 days of age, white pelage is present on the ventrum by 9–10 days, the pale-brown subadult pelage appears in days 13–18, and at about 12 weeks the gradual molt to the dark-brown color of the adult begins (Eisenberg, 1963).

The first appearances of various behavior patterns are: diagonal limb pattern of locomotion, 7–10 days; feeding on solids, 9 days; stretching, 9 days; shaking, 9 days; digging, 10 days; quadrupedal hop, 11–16 days; complete washing, 13 days; and scratching, 15 days. There is active grooming among siblings at 14 days, the weaning period is 21–24 days, driving and mounting begins at about 35 days, and they first leave the burrow at about 14–18 days. The cry of abandoned young wanes at 15–18 days, retrieving by the female wanes around 18 days, and the onset of activity outside the burrow begins from 18 to 21 days (Eisenberg, 1963).

In the laboratory, young females begin to show vaginal swelling and opening at 6 weeks. One female conceived at 12 weeks and delivered two young. Young males have well-descended testes at 3 months, but whether they have viable sperm is unknown (Eisenberg, 1963).

ECOLOGY. Generally, *D. nitratoides* inhabits arid, often strongly alkaline, plains sparsely clothed with grass and in places *Atriplex* (Fig. 4; Grinnell, 1933). Typical vegetation includes grasses and herbs, with *Ephedra* in the Panoche Valley being replaced in the San Joaquin Valley by more xerophylic shrubs (Eisenberg, 1963).

The area occupied by *D. n. exilis* is entirely on the flat floor of the San Joaquin Valley. Annual rainfall is <23 cm, falling mainly from November to February. During the rainy season, depressions in some of the habitat are temporary ponds, some of which are of considerable extent. Because of lack of drainage, the soil is heavily alkaline, especially in the low places where the surface bakes hard in the summer. No burrowing animals occupy these depressions. Soil of the elevated portions also is alkaline, but it is fine textured and often the surface is a powdery dust. In this habitat, the only vegetation is on the slightly elevated humps and consists mainly of grasses and *Suaeda moquini*. This soil is easily dug and is occupied

by San Joaquin kangaroo rats. Another type of terrain occupied by *D. nitratoides* consists of flat, irregular strips of hummocks. This soil is better drained and less alkaline. The surface is hard in summer, but is easy to dig. Vegetation is more abundant, with scattered clumps of *Atriplex*. Winter rains bring heavy growth of grasses and winter annuals; *Lepidium nitidum*, *Capsella bursa-pastoris*, and *Erodium* are abundant (Culbertson, 1946).

Burrows (Fig. 4) usually are at the base of some low bush, and runways, worn in the grass, often lead from one burrow to neighboring clumps of vegetation. Burrow entrances are 6–8 cm in diameter (Eisenberg, 1963). Burrow systems are on elevated soil, with entrance openings often located so the excavated dirt is thrown onto the surrounding alkaline soil. A burrow system may occupy an entire grass patch 2–3 m across. In summer, the first 15–20 cm of the surface soil is hard. Beneath this layer, the soil is loose and easily dug. The amount of dirt excavated is small, so that even over a long period of time there is no mound formed. When *Atriplex* and *Allenrolfea occidentalis* are widely scattered, *D. nitratoides* does not build burrows under them; however, in denser stands it burrows beneath them (Culbertson, 1946).

Burrow systems occur in a variety of soil conditions. Although *D. nitratoides* reportedly does not occur where the soil is heavy or in rocky soils (Culbertson, 1946), it is found on rocky hillsides on the Elkhorn Plain (D. F. Williams, pers. comm.). The area occupied by a burrow system varies from about 2 by 2 m to 3.5 by 3.5 m. Surface openings are either slanting or vertical and are of varying number. There usually is one vertical opening through which no dirt has been thrown out, but which is excavated by the animal from the inside; it may be full size and open, plugged, or only partly finished. These serve as escape openings or exits. There usually are several slanting openings; usually only two in use. Openings in use may show no newly excavated dirt for long periods of time. For one den, which covered an area of 2 by 2 m, some new dirt had been excavated from the softer layer under the hard top layer. Tunnels were 5 cm in diameter and 20–25 cm below the surface. One enlarged pocket (12.5 by 12.5 cm) was 14 cm beneath the surface. Another pocket was 15 cm below the surface. The bottoms of the shallow tunnels were dry and dusty, while the deeper ones and the pockets had the bottoms covered with damp soil. Soil in the pockets also was mixed with seed hulls. There was no nesting material and no stored food. Another system had a surface area of 3 by 3 m, one opening went down 60 cm, and a blind side pocket was 20 cm below the surface and was covered on the bottom with damp soil mixed with seed hulls (Culbertson, 1946).

The dampness of the burrow system may inhibit *D. nitratoides* from caching food in its burrow through part of the year. Seeds cannot be kept dry enough to keep them from sprouting or molding (Culbertson, 1946). However, this species does cache food (Eisenberg, 1967b.) Small pit caches are made in the walls of the burrow system. The dampness of the soil may influence the locus and amount of caching (Culbertson, 1946).

The San Joaquin kangaroo rat is a granivore (Eisenberg, 1967b). It feeds on seeds of such annuals as *Erodium* and *Capsella bursa-pastoris*, and shrubs such as *Atriplex* (Jameson and Peeters, 1988). In the spring, early rains cause growth of grasses and herbs (*Bromus*, *Festuca*, *Erodium*, and *Avena*) that form a food source (Eisenberg, 1963).

In San Benito County, the abundance of *D. nitratoides* appears to be in association with *Ephedra* on rolling hills. Gentle slopes, ridge tops, smooth terrain, distance from steep hills, and shrubby conditions make up the habitat where *D. nitratoides* is most common. The most prominent plants include *Bromus rubens*, *Erodium cicutarium*, *Ephedra californica*, *Lepidium nitidum*, and *Poa scabrella*. *D. ingens* is the most common kangaroo rat in more open areas and *D. heermanni* is the most common on steep slopes (Hawbecker, 1951).

On the Carrizo Plain, San Luis Obispo County, *D. nitratoides* frequented the same trap stations as *D. ingens* and *Perognathus inornatus* (Braun, 1985). Other associated mammals include *Spermophilus beecheyi*, *Ammospermophilus nelsoni*, *Thomomys bottae*, *Chaetodipus californicus*, *Onychomys torridus*, *Peromyscus maniculatus*, *Sylvilagus audubonii*, *Lepus californicus* (Hawbecker, 1951), and *Reithrodontomys megalotis* (Culbertson, 1946). Potential avian and mammalian predators include *Tyto alba*, *Taxidea taxus*, *Vulpes macrotis*, *Canis latrans*, *Lynx rufus*, and *Mustela frenata* (Hawbecker, 1951). Reptiles occurring in the same area include *Phrynosoma platyrhinos*, *Crotaphytus wislizenii*, *Uta*

stansburiana, Sceloporus occidentalis, Cnemidophorus tigris, Coluber constrictor, Pituophis melanoleucus, Crotalus viridus (Morrell, 1972), *Rhinocheilus lecontei,* and *Lampropeltis getulus* (Culbertson, 1946).

Ectoparasites include: the fleas *Meringis parkeri, Monopsyllus wagneri, Thrassis aridis* (Hardy et al., 1974a), and *Meringis californicus* (Hopkins and Rothchild, 1962); the ticks *Dermacentor parumapertus* (Hardy et al., 1974a) and *Ixodes jellisoni* (Furman and Loomis, 1984); the mite *Geomylichus multistriatus* (Fain et al., 1988); and the trombiculid chigger *Dermadelema mojavense* (Pomeroy and Loomis, 1984). Other parasites are the flagellate protozoan *Tritrichomonas muris* (Doran, 1953b) and the cestode *Hymenolepis citelli* (Simpson and Harmon, 1968). An attempt to infect *D. nitratoides* with the cestode *Oochoristica deserti* was not successful (Millemann, 1953). No coccidians were found in 29 specimens from Kern County (Hill and Best, 1985). Of 21 examined, none were naturally infected with *Eimeria mohavenis,* which parasitizes the lower small intestine and all of the caecum; however, 11 of 12 inoculated in the laboratory were successfully infected (Doran, 1953a). *D. nitratoides* can be infected with Buttonwillow virus, Modoc virus, Powassan virus, St. Louis encephalitis, and western equine encephalitis. However, no virus has been isolated from them or from fleas and ticks collected from their burrows (Hardy et al., 1974a). Only one of six *D. nitratoides* became infected when inoculated with Buttonwillow virus (Hardy et al., 1972). When inoculated with western equine encephalomyelitis virus, *D. nitratoides* was readily infected, and the infection usually was fatal (Hardy et al., 1974b).

Much of the habitat of *D. nitratoides* has been destroyed by farming activities (Culbertson, 1934, 1946). This species is not able to maintain its burrow systems and live in areas under irrigation and cultivation. However, it will re-invade fields no longer cultivated (Culbertson, 1946). *D. n. exilis* and *D. n. nitratoides* are listed as endangered by the U.S. Fish and Wildlife Service. In addition, *D. n. brevinasus* is listed as a species of special concern by the California Department of Fish and Game (J. R. Gustafson, pers. comm.).

BEHAVIOR. The San Joaquin kangaroo rat is nocturnal and does not hibernate (Eisenberg, 1967b). Though nocturnal, they have been captured in traps 5 min before sunset. In one study, *D. nitratoides* emerged from its burrow about 6 min past sundown, which was 5–12 min earlier than *D. heermanni* in the same area (Tappe, 1941). In laboratory trials, *D. nitratoides* showed no significant difference in activity under full-moon and new-moon simulations. However, the moon did affect activity with respect to rise and set. The average duration of activity after moonrise was less than before moonrise, and less before moonset than after moonset (Lockard and Owings, 1974).

The species is solitary and separate, except during estrus (Eisenberg, 1967b). When two or more San Joaquin kangaroo rats are placed in the same cage, fighting ensues. They will stand on their hind feet, sniff, leap, and attempt to kick and bite each other. However, none were killed when six males were placed in the same cage; the following morning all were huddling together (Culbertson, 1946). When kept in crowded laboratory conditions, there is extended fighting among adults and abandonment of the young by mothers (Eisenberg, 1967b). Responses between males and females change cyclically as the female passes through estrus (Eisenberg, 1963).

Mating behavior involves a preliminary period of mutual investigation, often mixed with agonistic patterns. The male begins to follow and drive the female, making attempts to mount. The female assumes a "frozen" posture, often when the male is not in contact with her. Mounting and thrusting occur in bouts and several bouts probably precede ejaculation. After ejaculation, the animals separate and wash their perineal regions. During copulation there is a neck grip and multiple mounts in a series (Eisenbeg, 1963). Copulation usually involves three mounts lasting 60–150 s. Intervals between mounts last 30–120 s and the total duration of mounts and intervals is about 8.5 min (Eisenberg, 1967b). Speed of pelvic thrusts is 1/s; the male does not fall to one side at the conclusion of the mount. Apparently the male ejaculates only once, since after a terminal mount the male either expresses no further interest in the female or mounts after about 10 min without seeming to attain intromission, thrusting in a feeble manner (Eisenberg, 1963). This long copulatory period may have developed if copulation occurs underground in burrows (Eisenberg, 1967b).

It appears that *D. nitratoides* establishes a contact relationship before or at the time of copulation. Individuals tend to nest separately after copulation, but in the caged situation the male re-establishes contact and cohabits with the female until shortly before parturition, when she drives him out. In the wild, the animals probably pair for a short time at the time of copulation and then separate and stay separated throughout pregnancy (Eisenberg, 1963).

On the day preceding the birth, the female generally is quite active. Both nest building and caching are carried on to great lengths. This manipulative activity appears to remain intense for 1 or 2 days after parturition. Behavioral components during the birth process include: stretching by the mother; pulling the neonate from the birth canal using the incisors and the forepaws; removing blood and mucus from the neonate while grooming with the forepaws, teeth, and tongue; and eating the placenta (Eisenberg, 1963).

In caring for the young, the female crouches over the young, keeping her back arched to prevent crushing them. This allows the young to nurse while they are kept warm. The female continues grooming and the removal of the neonate's feces and urine by licking the anal and genital regions. In handling the young, the female employs several fundamental patterns; pulling under, patting, and pushing. A young that has wandered out of the nest is picked up by a fold of skin with the incisors and carried back to the nest. The female initially may seize the skin anywhere on the neonate's body, but generally shifts to carry it by the skin of the back (Eisenberg, 1963).

Nonvocal auditory communication includes tooth-chattering and foot-drumming. Vocalizations include growls, squeals, and low grunts (Eisenberg, 1963).

Sandbathing sequences of behavior indicate that belly-rub sequences tend to contain more acts than sequences of side rubbing, there is a tendency to integrate side and belly rubs, and an extended sequence is likely to begin with a side rub, continue with belly rubs, and end with side rubs. There tend to be acts in a sequence involving one side or the belly; they will rub one side two or three times before changing to the alternate side or to the belly (Eisenberg, 1963).

When digging, *D. nitratoides* stands firmly on its hind legs, which are spread well apart, and scratch rapidly with the front feet. The dirt is pushed back under the body, and then the dirt is sent flying backwards with several strong kicks with the hind legs. As the burrow becomes deeper, the dirt accumulates and gets in the way. Then, the animal turns around, comes out of the opening, and pushes the dirt a little with the front feet. When it turns and starts down the burrow it kicks backward, scattering dirt away from the opening. On the next trip to the opening, the accumulated dirt is kicked backward as the animal moves backward. This backward moving and kicking carries the dirt some distance from the opening. As the animal returns to the entrance, there also is some kicking of the dirt all the way. Each successive trip moves the dirt farther away and in different directions, resulting in a more or less fan-shaped distribution. Mounds of any size would be a hindrance, interfering with the rapid entrances the animals must make when pursued or frightened (Culbertson, 1946).

Though kangaroo rats are excellent swimmers (Stock, 1972), *D. nitratoides* is notably averse to getting wet. When San Joaquin kangaroo rats get wet, they immediately will rub and roll in a dusty place to dry themselves. The tail is groomed by rapidly running it through the front paws as they are held against the mouth (Culbertson, 1946).

GENETICS. The diploid number of chromosomes is 54 (Fig. 5) and the fundamental number of chromosomes arms is 104. There are 3 pair of metacentric chromosomes, 20 pair of submetacentrics, 3 pair of subtelocentrics, the X chromosome is submetacentric, and the Y chromosome is acrocentric (Stock, 1974).

Genic analysis revealed the mean number of alleles per locus was 1.22, the mean proportion of loci polymorphic per population was 0.22, and the mean proportion of loci heterozygous per individual was 0.040. *D. nitratoides* has a high level of variability (Johnson and Selander, 1971). 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. nitratoides:* principal, 41; intermediate, 29; and two satellite DNA components totaling 30% (Mazrimas and Hatch, 1972). The distribution of DNA buoyant density fractions in neutral cesium chloride differs from other species of *Dipodomys* (Hatch et al., 1976).
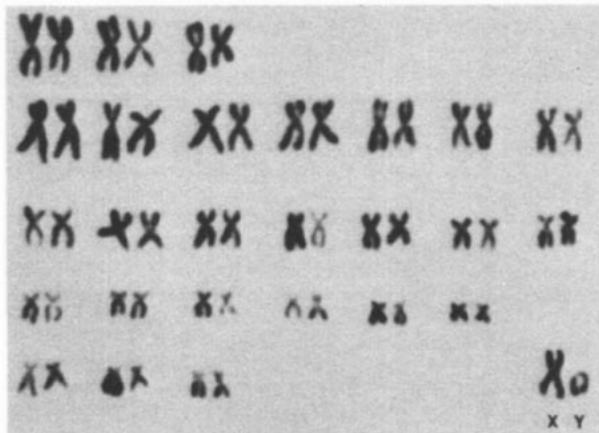
FIG. 5. Karyotype of *Dipodomys nitratoides* (Hsu and Benirschke, 1975).

REMARKS. Attempts have been made to arrange *Dipodomys* into groups that are intended to show relationships. Grinnell (1921) placed *D. nitratoides* in the *merriami* group with *D. merriami, D. margaritae,* and *D. insularis.* Subsequent studies to elucidate relationships between *D. nitratoides* and other species of *Dipodomys* have examined: skeletal and visceral measurements (closest affinities are with *D. merriami, D. margaritae, D. insularis, D. phillipsii,* and *D. elator;* Setzer, 1949); field experience (*D. insularis, D. merriami,* and *D. margaritae;* Lidicker, 1960a); structure of the molariform teeth (*D. deserti, D. merriami, D. heermanni,* and *D. ordii;* Nader, 1966); protein variation (*D. merriami;* Johnson and Selander, 1971; Patton et al., 1976); percent of satellite DNA compared to indices derived from lengths of limb bones (*D. ingens, D. heermanni,* and *D. merriami;* Mazrimas and Hatch, 1972); percent of satellite plus intermediate DNA and the fundamental number of chromosome arms (*D. merriami;* Mazrimas and Hatch, 1972); bacula (not closely associated with any other species; Best and Schnell, 1974); chromosomes (*D. merriami;* Stock, 1974); phenetic analyses of skeletal characters (*D. merriami;* Schnell et al., 1978); and phenetic analyses of cranial characters (*D. merriami* and *D. margaritae;* Best, in press).

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. According to D. F. Williams (pers. comm.), the name *nitratoides* probably refers to the similarity between this species and *D. merriami nitratus,* which Merriam (1894) named from a locality east of Owens Lake. The type locality of *D. m. nitratus* has soils with large amounts of calcium carbonate; the Latin root *nitr* is derived from *natron* meaning native soda or calcium carbonate. By dropping the *us* of *nitratus* and adding the Greek *oides,* the resulting word *nitratoides* means "a thing like *nitratus.*"

H. T. Haagenstad prepared Fig. 3. The California Department of Fish and Game granted permission for me to capture and photograph this species. F. S. Dobson, J. L. Dobie, R. S. Lishak, J. O. Whitaker, Jr., and D. F. Williams critically evaluated an early draft of the manuscript. This is journal article no. 15-902413P of the Alabama Agricultural Experiment Station.

LITERATURE CITED

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

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

———. In press. Patterns of morphologic and morphometric variation in heteromyid rodens. *In* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists, 10.

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

BOOLOOTIAN, R. A. 1954. An analysis of subspecific variations in *Dipodomys nitratoides.* Journal of Mammalogy, 35:570–577.

BRAUN, S. E. 1985. Home range and activity patterns of the giant kangaroo rat, *Dipodomys ingens.* Journal of Mammalogy, 66: 1–12.

BURT, W. H. 1960. Bacula of North American mammals. Miscellaneous Publications, Museum of Zoology, University of Michigan, 113:1–76.

CULBERTSON, A. E. 1934. Rediscovery of Dipdomys nitratoides exilis. Journal of Mammalogy, 15:161–162.

———. 1946. Observations on the natural history of the Fresno kangaroo rat. Journal of Mammalogy, 27:189–203.

DORAN, D. J. 1953a. Coccidiosis in the kangaroo rats of California. University of California Publications in Zoology, 59:31–60.

———. 1953b. The occurrence of *Tritrichomonas muris* (Grassi) in heteromyid and cricetid rodents of California. The Journal of Parasitology, 39:569.

EISENBERG, J. F. 1963. The behavior of heteromyid rodents. University of California Publications in Zoology, 69:1–100.

———. 1967a. The heteromyid rodents. Pp. 391–395, *in* The UFAW handbook on the care and management of laboratory animals (W. Lane-Petter, A. N. Worden, B. F. Hill, J. S. Paterson, and H. G. Vevers, eds.). E. and S. Livingstone Ltd., London, 1015 pp.

———. 1967b. A comparative study in rodent ethology with emphasis on evolution of social behavior, I. Proceedings of the United States National Museum, 122:1–51.

EISENBERG, J. F., AND D. E. ISAAC. 1963. The reproduction of heteromyid rodents in captivity. Journal of Mammalogy, 44: 61–67.

FAIN, A., J. O. WHITAKER, JR., AND H. H. THOMAS. 1988. Two new species of *Geomylichus* Fain, 1970 (Acari, Listrophoridae) from California, U.S.A. International Journal of Acarology, 14: 121–125.

FITZINGER, L. J. 1867. Versuch einer natürlichen anordnung der nagethiere (Rodentia). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Wien, Abtheilung 1, 56:57–168.

FURMAN, D. P., AND E. C. LOOMIS. 1984. The ticks of California (Acari: Ixodida). Bulletin of the California Insect Survey, 25: 1–239.

GAMBEL, W. 1848. Descriptions of two new California quadrupeds. Proceedings of the Academy of Natural Sciences of Philadelphia, 4:77–78.

GRAY, J. E. 1841. A new genus of Mexican glirine Mammalia. Annals and Magazine of Natural History, Series 1, 7:521–522.

GRINNELL, J. 1920. A new kangaroo rat from the San Joaquin Valley, California. Journal of Mammalogy, 1:178–179.

———. 1921. Revised list of the species in the genus Dipodomys. Journal of Mammalogy, 2:94–97.

———. 1922. A geographical study of the kangaroo rats of California. University of California Publications in Zoology, 24: 1–125.

———. 1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology, 40:71–234.

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

HAMILTON, M .J., R. K. CHESSER, AND T. L. BEST. 1987. Genetic variation in the Texas kangaroo rat, *Dipodomys elator* Merriam. Journal of Mammalogy, 68:775–781.

HARDY, J. L., R. N. LYNESS, AND W. A. RUSH. 1972. Experimental vector and wildlife host ranges of Buttonwillow virus in Kern County, California. The American Journal of Tropical Medicine and Hygiene, 21:100–109.

HARDY, J. L., W. C. REEVES, W. A. RUSH, AND Y. D. NIR. 1974a. Experimental infection with western equine encephalomyelitis virus in wild rodents indigenous to Kern County, California. Infection and Immunity, 10:553–564.

HARDY, J. L., W. C. REEVES, R. P. SCRIVANI, AND D. R. ROBERTS. 1974b. Wild mammals as hosts of group A and group B arboviruses in Kern County, California: a five-year serologic and virologic survey. The American Journal of Tropical Medicine and Hygiene, 23:1165–1177.

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.

HATT, R. T. 1932. The vertebral columns of ricochetal rodents.

Bulletin of the American Museum of Natural History, 63:599–738.

HAWBECKER, A. C. 1951. Small mammal relationships in an Ephedra community. Journal of Mammalogy, 32:50–60.

HILL, T. P., AND T. L. BEST 1985. Coccidia from California kangaroo rats (*Dipodomys* spp.). The Journal of Parasitology, 71:682–683.

HOFFMANN, W. M. 1975. Geographic variation and taxonomy of *Dipodomys nitratoides* from the California San Joaquin Valley. M.A. thesis, California State University, Fresno, 75 pp.

HOPKINS, G. H. E., AND M. ROTHCHILD. 1962. An illustrated catalogue of the Rothchild collection of fleas (Siphonaptera) in the British Museum (Natural History) with keys and short descriptions for the identification of families, genera, species and subspecies of the order. III. Hystrichopsyllidae (Acedestiinae, Anomiopsyllinae, Hystrichopsyllinae, Neopsyllinae, Rhadinopsyllinae and Stenoponiinae). British Museum (Natural History), London, 560 pp.

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

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

JAMESON, E. W., JR., AND H. J. PEETERS. 1988. California mammals. University of California Press, Berkeley, 403 pp.

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

JONES, W. T. 1985. Body size and life-history variables in heteromyids. Journal of Mammalogy, 66:128–132.

KELLY, T. S. 1969. The comparative morphology of the male phallus in the genus *Dipodomys*. M.S. thesis, San Fernando Valley State College, Northridge, California, 133 pp.

KENAGY, G. J. 1973. Adaptations for leaf eating in the Great Basin kangaroo rat, *Dipodomys microps*. Oecologia, 12:383–412.

KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

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

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

LOCKARD, R. B., AND D. H. OWINGS. 1974. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. Animal Behaviour, 22:262–273.

MAYER, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. The American Midland Naturalist, 48:480–512.

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 Biology, 240:102–105.

MERRIAM, C. H. 1890. Annotated list of mammals of the San Francisco Mountain plateau and desert of the Little Colorado in Arizona, with notes on their vertical distribution, and descriptions of new species. North American Fauna, 3:43–86.

———. 1894. Preliminary descriptions of eleven new kangaroo rats of the genera Dipodomys and Perodipus. Proceedings of the Biological Society of Washington, 9:109–115.

MILLEMAN, R. 1953. Studies on the biology of the cestode *Oochoristica deserti* n. sp. Ph.D. dissert., University of California, Los Angeles, 89 pp.

MORRELL, S. 1972. Life history of the San Joaquin kit fox. California Fish and Game, 58:162–174.

NADER, I. A. 1966. Roots of teeth as a generic character in the kangaroo rat, *Dipodomys*. Bulletin of the Biological Research Centre, Baghdad, 2:62–69.

PATTON, J. L., H. MACARTHUR, AND S. Y. YANG. 1976. Systematic relationships of four-toed populations of *Dipodomys heermanni*. Journal of Mammalogy, 57:159–163.

POMEROY, L. V., AND R. B. LOOMIS. 1984. A new genus of trombiculine chiggers (Acari: Trombiculidae) from western North America. Journal of Medical Entomology, 21:268–273.

PYE, A. 1965. The auditory apparatus of the Heteromyidae (Rodentia, Sciuromorpha). Journal of Anatomy, 99:161–174.

QUAY, W. B. 1960. The pancreatic islets of desert rodents. The American Midland Naturalist, 64:342–348.

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

SCHNELL, G. D., T. L. BEST, AND M. L. KENNEDY. 1978. Interspecific morphologic variation in kangaroo rats (*Dipodomys*): degree of concordance with genic variation. Systematic Zoology, 27:34–48.

SETZER, H. W. 1949. Subspeciation in the kangaroo rat, Dipodomys ordii. University of Kansas Publications, Museum of Natural History, 1:473–573.

SIMPSON, R. L., AND W. HARMON. 1968. Occurrence of *Hymenolepis citelli* McLeod, 1933 in the rodent genus *Dipodomys* Gray, 1841. The Journal of Parasitology, 54:769.

STOCK, A. D. 1972. Swimming ability in kangaroo rats. The Southwestern Naturalist, 17:98–99.

———. 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. Journal of Mammalogy, 55:505–526.

TAPPE, D. T. 1941. Natural history of the Tulare kangaroo rat. Journal of Mammalogy, 22:117–148.

WILLIAMS, D. F., AND H. H. GENOWAYS. In press. Taxonomy of the heteromyid rodents. *In* Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication, the American Society of Mammalogists, 10.

WOOD, A. E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Annals of the Carnegie Museum, 24:73–262.