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Dipodomys heermanni.

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Dipodomys heermanni Le Conte, 1853

Heermann's Kangaroo Rat

D[*ipodomys*]. *heermanni* Le Conte, 1853:224. Type locality "Sierra Nevada [probably in the Upper Sonoran Life-zone on the Calaveras River, Calaveras Co., California]" (Grinnell, 1922:47).

Perodipus streatori Merriam, 1894:113. Type locality "Carbondale, Amador [not Mariposa] County [California]" (Grinnell, 1922:47).

Perodipus goldmani Merriam, 1904:143. Type locality "Salinas, mouth of Salinas Valley, Monterey Co. [California]."

Perodipus morroensis Merriam, 1907:78. Type locality "Morro, San Luis Obispo Co. [California]."

Perodipus swarthi Grinnell, 1919*a*:44. Type locality "seven miles southeast of Simmler, Carrizo Plain, San Luis Obispo County, California."

Perodipus dixoni Grinnell, 1919*a*:45. Type locality "Delhi, near Merced River, Merced County, California."

Dipodomys jolonensis Grinnell, 1919*b*:203. Type locality "valley floor one mile southwest of Jolon [Monterey Co., California]."

Dipodomys berkeleyensis Grinnell, 1919*b*:204. Type locality "top of hill at [the former] head of Dwight Way, Berkeley [Alameda Co., California]."

Dipodomys tularensis, Merriam, 1904:143. Type locality "Alila [now Earlimart], Tulare Co., California."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae. Following Patton et al. (1976), nine subspecies are recognized:

D. h. arenae Boulware, 1943:392. Type locality "C. A. Davis Ranch, 2 mi. NNW Lompoc, 400 ft., Santa Barbara Co., California."

D. h. berkeleyensis Grinnell, 1919*b*:204, see above.

D. h. dixoni (Grinnell, 1919*a*:45), see above.

D. h. goldmani (Merriam, 1904:143), see above.

D. h. heermanni Le Conte, 1853:224, see above (*streatori* Merriam is a synonym).

D. h. jolonensis Grinnell, 1919*b*:203, see above.

D. h. morroensis (Merriam, 1907:78), see above.

D. h. swarthi (Grinnell, 1919*a*:44), see above.

D. h. tularensis (Merriam, 1904:143), see above.

DIAGNOSIS. *Dipodomys heermanni* is a medium-sized kangaroo rat (Fig. 1). It is a "broad-faced" species (Grinnell, 1922); the maxillary arches are wide (4.0 to 6.0 mm) and are well spread from the longitudinal axis of the skull (Fig. 2). The width across the maxillary roots is greater than 54.8% of the greatest length of the skull (Hall, 1981). The posteroexternal angle of the maxillary arches is prominent (Grinnell, 1922). Heermann's kangaroo rat possesses five toes on each hind foot. This feature alone distinguishes the species from the similar *D. californicus* where their ranges meet in central California, and from the smaller *D. nitratoides* where they co-occur in southwestern California. *D. ingens* is largest and heaviest of the kangaroo rats, and may be distinguished from *D. heermanni* primarily on the basis of size (Grinnell, 1922; Hall, 1981). All remaining sympatric species of kangaroo rats are in Lidicker's (1960*a*) *agilis*-subgroup of the *heermanni* group, and are most readily characterized as being "narrow-faced" (Grinnell, 1922). Additionally, *D. agilis* generally is darker than subspecies of *D. heermanni* with which it is sympatric. Both *D. venustus* and *D. elephantinus* may be distinguished by their large ears and larger size than co-occuring *D. heermanni* (Grinnell, 1922).

GENERAL CHARACTERS. The pelage in *D. heermanni* is long and silky. The general color pattern is typical of that for *Dipodomys* in general (Hall, 1981). The dorsal body surface in this species ranges in color from tawny-olive strongly overwashed with black (*D. h. morroensis*), to ochraceous-buff (*D. h. swarthi*; Grinnell, 1922), although albino specimens are known (von Bloeker, 1930). The characteristic hip stripe that separates the darker thighs and dorsum in most *Dipodomys* is absent in roughly 5% of *D. h. arenae* and over 75% of *D. h. morroensis* (A. I. Roest, in litt.). The tail crest ranges from black with a sharply demarcated white tip in some *D. h. heermanni* (these may be *D. californicus*), to dusky and only slightly crested in *D. h. dixoni*, *D. h. berkeleyensis*, and most *D. h. heermanni*, to dusky or blackish and very scantily haired in *D. h. goldmani* and *D. h. morroensis* (Grinnell, 1922). The dorsal guard hairs are oval and taper abruptly; they are unbanded and possess well-developed medullary aggregations located in individual invaginations in the medullary substance (Homan and Genoways, 1978; Mayer, 1952). These hairs are usually 13 mm or less in length (if 13 mm, then medullary aggregations are not more than three abreast); cortical pigmentation is prominent for <4 mm along the length of the shaft. In *D. h. goldmani* the dorsal guard hairs have a maximum length of 15 mm, width to 45 μm, and medullary (not cortical) pigmentation is dark for the distal fraction of a mm, and this is subtended by a 2 mm black band (Mayer, 1952).

External measurements (in mm) are as follows (Grinnell, 1922): total length, 250 to 313; length of tail, 160 to 200; length of hind foot, 38 to 46; length of ear, 10 to 17. Average greatest length of skulls ranges from 37.0 mm in *D. h. dixoni* to 41.6 mm in *D. h. jolonensis*; average greatest breadth across the bullae ranges from 23.2 mm in *D. h. dixoni* to 25.8 mm in *D. h. swarthi* (Grinnell, 1922). Means of selected cranial measurements (in mm; males and females, respectively are (Best, in press): basal length 22.6, 22.4; greatest length, 40.2, 39.7; maxillary arch spread, 22.4, 22.2; interorbital width, 11.1, 11.0; nasal length, 14.8, 14.6; basioccipital length, 5.9, 5.8; greatest depth, 13.5, 13.3; greatest width, 24.9, 24.6; zygomatic width, 20.4, 20.1; nasal width, 4.0, 3.9.

With 474 adult males and 355 adult females, Best (in press) found significant sexual dimorphism in all standard external measurements and most cranial measurements analyzed, with males larger in all of them. Samples of only 20 males and 20 females demonstrated dimorphism only in the maxillary arch spread and intermaxillary width.

DISTRIBUTION. *Dipodomys heermanni* occurs in California south from a line roughly extending between Suisun Bay and

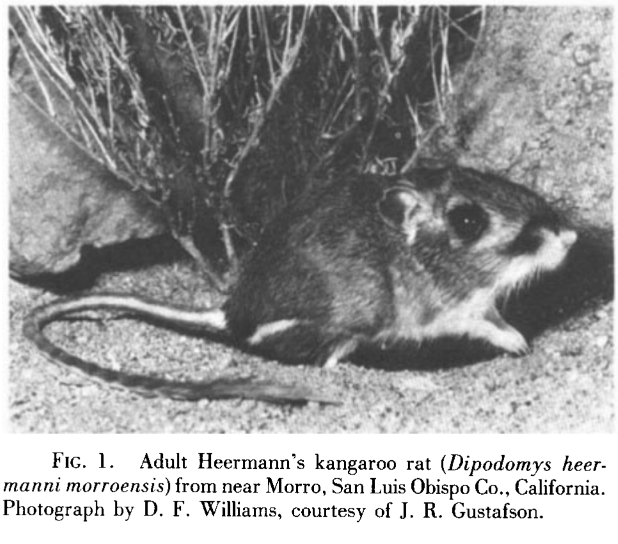

FIG. 1. Adult Heermann's kangaroo rat (*Dipodomys heermanni morroensis*) from near Morro, San Luis Obispo Co., California. Photograph by D. F. Williams, courtesy of J. R. Gustafson.

FIG. 2. Dorsal, ventral, and lateral views of the skull, and a lateral view of the mandible of an adult female *Dipodomys heermanni tularensis* (Field Museum of Natural History 12925) from Ft. Tejon, Kern Co., California. Greatest length of cranium is 38.2 mm. Photos by C. Garner.

Lake Tahoe, to slightly north of Pt. Conception, and west from the foothills of the Sierra Nevada and Tehachapi mountains to the Pacific Ocean (Fig. 3: Grinnell, 1922; Hall, 1981). *D. heermanni* is not known from the fossil record.

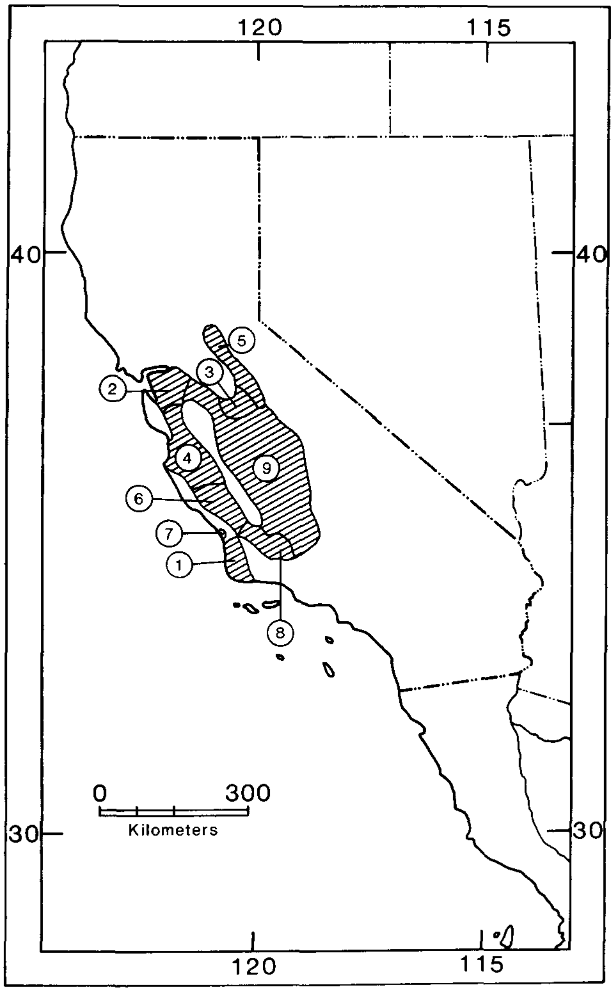

FIG. 3. Distribution of *Dipodomys heermanni* in California. Subspecies boundaries from Hall (1981) and A. I. Roest (in litt.): 1, *D. h. arenae*; 2, *D. h. berkeleyensis*; 3, *D. h. dixoni*; 4, *D. h. goldmani*; 5, *D. h. heermanni*; 6, *D. h. jolonensis*; 7, *D. h. morroensis*; 8, *D. h. swarthi*; 9, *D. h. tularensis*. Map prepared by C. Garner.

FORM AND FUNCTION. *Dipodomys heermanni* possesses relatively large sebaceous glands, small mucous glands, and no sudoriferous (apocrine) glands (Quay, 1965). In contrast to some other species, the large middorsal sebaceous gland in *D. heermanni* secretes throughout the year in 90% of adults, with no significant sexual dimorphism and little seasonal variation in secretion. There is no apparent relationship between either gland size or activity and molt or breeding season (Quay, 1953).

The dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20 (McLaughlin, 1984). Lengths of mandibular and maxillary toothrows for small samples average 5.2 and 4.9 mm, respectively (Boulware, 1943; Wood, 1935). The vertebral formula in *D. heermanni* (Hatt, 1932) is: cervical, 7; thoracic, 12; lumbar, 7; sacral, 2; pseudosacral, 3 (occasionally 2); caudal, 30 to 32; total, 60 to 62 (this count may not be complete).

The baculum of *D. heermanni* is relatively large proximally and tapers gradually to the distal end, which curves downward (Burt, 1936). Of 11 species analyzed (Lidicker, 1960*b*), only 2 (*D. agilis* and *D. ingens*) had more robust bacula than *D. heermanni*. Mean values (in mm) for bacula of *D. heermanni* are: length, 11.5 (n = 17); width of base, 1.5 (n = 14); height at base, 2.0 (n = 14; Best and Schnell, 1974).

Setzer (1949) found the myology of *D. heermanni* to agree in detail as to origin, insertion, and innervation with that of Howell's (1932) study of *D. spectabilis*. He (Setzer, 1949) also found Midgely's (1938) description of the viscera of *D. ordii* and *D. microps* to apply to *D. heermanni*.

Dipodomys heermanni has a small stomach capacity relative to other rodents (Fitch, 1948). In 19 kangaroo rats trapped between November and January, the stomach (including contents) averaged only 2.14% (range, 0.8 to 3.3) of body mass. *D. heermanni* has the smallest ratio of small intestine to large intestine of all kangaroo rats studied: 165/432 mm = 38.2% (Setzer, 1949). The caecum is large. The large intestine is long and highly coiled. Morphologically, *D. heermanni* seems to be a generalized kangaroo rat, only moderately specialized in most characters (Setzer, 1949).

Intrapalmar subdermal injections of acetylcholine (2 mg in 50 μl) stimulate palmar sweat glands, whereas NaCl (50 μl of 0.9%) has no effect (Quay, 1966). Insulin increases mean diaphragm glucose output (Kelley and Quay, 1970). Succinic dehydrogenase was found in *D. heermanni* ($n = 6$) to reduce 253.5 ± 16.4 μM of tetrazolium/μg of dry tissue (Quay, 1960*a*). Alpha cells in the pancreatic islets in this species tend to be located centrally; the alpha/beta ratio is high relative to many rodents (25% in *D. heermanni*; $n = 1$), although apparently not for desert species (Quay, 1960*b*). *D. heermanni* possesses a complex system of hypothalamic and peripheral temperature receptors (Sakaguchi et al., 1979). A 60 g field-trapped Heermann's kangaroo rat placed in a refrigerator at −5° to −1° C for 24 h lost approximately 1 g, but otherwise appeared healthy (Howard, 1951).

ONTOGENY AND REPRODUCTION. *Dipodomys heermanni* primarily breed from February to October (Fitch, 1948; Tappe, 1941); activity peaks in April and decreases after July (Fitch, 1948). Testes are abdominal in November and December, but enlarge and descend in January and February (Fitch, 1948); some individuals have descended testes in June (J. Congdon, in litt.). The gestation period is 30 to 32 days; if not impregnated, females will cycle every 18 to 20 days (A. I. Roest, in litt.). Pregnant females had an average of 3.8 (sample size not given; range, 2 to 5) embryos in San Juaquin and San Benito counties (Tappe, 1941). Litter sizes averaged 2.6 ($n = 14$; range 2 to 3), based partly on counts of young born in traps, in San Benito Co. (Fitch, 1948), and 3.33 ($n = 6$; range 3 to 4) in San Luis Obispo Co. (Stewart and Roest, 1960).

Specimens with testes >8 mm long have engorged penile blood sinuses. The glans is covered with an inner membrane that is tightly adherent in juveniles and nonbreeding adults, but loose in sexually active males. Penile spines develop when males become sexually active, and are regressed at other times (Kelly, 1969).

Young born at normal term are poikilothermic. Birth weights for these average 3.7 g ($n = 4$; range, 3.4 to 3.9 g; Tappe, 1941). Fitch (1948) reported birth weights to be 5 g, about 8% that of adults. Birth is head-first (Tappe, 1941). Neonates are moist at birth, but dry in minutes. Their skin is bright pink and wrinkled, and hairless except for prominent unpigmented vibrissae. Cranial sutures and blood vessels are clearly visible through the skin. Auditory and mastoid bullae are relatively small compared with the adult condition. The eyes, about 3 mm in diameter, are closed at birth. The pupils appear as pink dots approximately 1 mm in diameter. A shallow, horizontal groove across the center of the upper half of the eye marks the line of abscission (Tappe, 1941). Cheek pouches begin as shallow, crescent-shaped folds in the skin. The external ears are closed, and the pinnae are laid over the meatus. The hind limbs are approximately 33% longer than the forelimbs, and only slightly heavier, possessing a large fleshy hallux with short, soft nails that bleed if cut. The tail is relatively short, slightly greater than 50% the length of the head and body (Tappe, 1941). Young in a premature litter were born hairless except for pale yellow, 2-mm vibrissae (Tappe, 1941).

Dark and light areas of the juvenile skin correspond to those of the adult pelage. Pigmentation in developing hairs starts within 22 h of birth. Fine hairs appear on the back and top of the head on day 3 (Tappe, 1941); in some populations this does not appear until day 10 (Stewart and Roest, 1960). Pigmentation spreads over the head, back, tail, and limbs (in that order) by day 4, and obscures cranial sutures by day 6; pigmentation extends to the soles of the feet by day 7. As pigmentation progresses, the dermal gland appears as an elongate, smooth surfaced, unpigmented spot; it is not roughened as in the adult. At this time the swollen area on each side of the nose where the vibrissae arise remains bright pink; all other pigmented parts are dull pink. All pigmented areas are covered by juvenile pelage by day 9, whereas unpigmented areas are less densely covered with short fine hairs; the rest of the tail appears hairless. External genitalia are not differentiable until day 9. In males, a swelling appears on either side of the prepuce and a reddened ridge extends back from the prepuce. The swellings and the ridge are both absent in females (Tappe, 1941). Upper incisors erupt on day 11 or 12. Postjuvenile pelage appears on top of the head by day 12, extending to the shoulders by day 14, and to the back and rump by day 15. At 16 days, the lengths of the tail and the body are increasing at approximately the same rate. Head and body length almost doubles in the first 17 days; the tail and hind feet triple in length. At this time the length of the hind foot is approximately 75% adult size, the body is approximately 50% adult size, and the tail 33% adult size. The incisors change color from white to yellow by day 18. Pelage is similar to adults by 3 (San Juaquin Co.; Tappe, 1941) to 5 weeks (San Luis Obispo Co.; Stewart and Roest, 1960). Cheekteeth emerge on day 23 and are well developed by day 25. By one month, the tail is increasing in length faster than the head and body (Tappe, 1941). Tail growth approximates the simple allometric equation, y = xbk, where y equals tail length, x equals head and body length, b is a nonbiological constant, and k is the ratio of the relative growth rate of the tail to that of the body (Huxley, 1932). For young *D. heermanni*, Tappe (1941) calculated k = 1.73.

Weaning begins as soon as the young first start to take solid food (about day 17) and is completed by day 25 (Tappe, 1941). Weaning in captive young is completed by 25 or 26 days (Fitch, 1948; A. I. Roest, in litt.; Stewart and Roest, 1960). Juveniles are crawling by day 3, and can stand on their hind limbs by day 14. Movement is bipedal on day 20, and animals can hop on day 35. Young begin to forage for themselves by 4 weeks (Fitch, 1948), and to leave their burrows and perhaps seek new ones, by 4 to 6 weeks (Fitch, 1948; Tappe, 1941). The youngest trapped specimens in San Luis Obispo Co. were estimated to be 5 to 6 weeks old (Stewart and Roest, 1960). Tunneling begins around day 40, with young digging only small pits by scratching with their front feet. By 2 months, they dig tunnels from 15 to 20 cm long (Tappe, 1941). Adult weights are attained by 10 to 16 weeks (Fitch, 1948; Stewart and Roest, 1960; Tappe, 1941), and adult pelage by 17 to 20 weeks (Stewart and Roest, 1960).

ECOLOGY. The general habitat type includes both the Lower and Upper Sonoran life zones and at some places extends into the Transition zone (Grinnell, 1922). Although some subspecies concentrate on knolls and ridges where soil is shallow and well drained and vegetation is scanty (Fitch, 1948), others are found only on sandy valley floors or coastal plains (A. I. Roest, in litt.). The comparatively broad habitat requirements of this species possibly are correlated with its relatively high genic heterozygosity (Johnson and Selander, 1971).

Heermann's kangaroo rats frequently use tunnels of ground squirrels (*Spermophilus*); these may provide shelter from where they can dig their own tunnels (Fitch, 1948). The degree of burrowing is dependent upon soil structure. In areas with fine deep soils, tunnels average 10.7 m long, are 15 to 51 cm beneath the surface, and have numerous loops and side branches (Tappe, 1941). In sandy coastal soils, burrows are more simple, contain few branches, and are of depths usually <27 cm (A. I. Roest, in litt.). In shallow, rocky soils composed mostly of decomposing granite, tunnels have only a few short lateral pockets. Average length of these tunnels is 3.3 m, and none extend deeper than 19.4 cm (Fitch, 1948). Main entrances usually are situated under bushes or boulders. Burrows usually descend gradually and are considerably wider than the animal. Entrances are 4 to 8 cm wide ($\bar{X} = 6.2$ cm), and the width of underground burrows is 5 to 9 cm (Tappe, 1941). Other, narrower tunnels rise to the surface almost vertically. Animals first appear at night at these entrances before exiting at main entrances (Tappe, 1941). They probably are used for emergency escapes as well (Fitch, 1948). Nests usually are fairly odorless and clean of feces. Burrow plugs are approximately 5% feces. Fecal pellets are 5 to 7 by 2.5 mm, and are rounded or pointed at each end (Tappe, 1941).

Almost all burrows have at least one place nearby for dust-bathing. Dust baths are located beneath bushes or ledges when available, but more often occur in the open along trails or by an entrance. In some areas, the loose dirt excavated from the burrows is used for dust-bathing (Tappe, 1941).

The many interconnections of surface runways of different individuals indicate a lack of true territoriality in these kangaroo rats (Fitch, 1948). Home ranges appear to be variable in sizes. Population densities fluctuate yearly, usually between 2 to 30 kangaroo rats/ha (Fitch, 1948; A. I. Roest, in litt.). Fitch (1948) reported that 18% of recaptured individuals were within 30.5 m of their first capture site, and 37% were within 15 m. He considered the foraging range of an individual to be 30 to 122 m across. Large emigrations are irregular and unpredictable in both distance and time of occurrence, but evidently are more likely among 40 to 50 g individuals and are more common among females than males (Fitch, 1948).

Seeds of the following species are accepted by captive *D.*

heermanni and occur in at least 50% of the areas in which these animals are found (Stewart and Roest, 1960): *Coreothrogyne filaginifolia, Lotus scopularius, Circium occidentale, Potentilla lindleyi, Chorizanthe californica, Salvia mellifera, Ericameria ericoides, Dudleya caespitosa, Lupinus chamissoni*, and *L. arboreus*. Other species known to be fed upon include *Erodium cicutarium, Croton californicus, Erigonum parvifolium, Abronia umbellata, Eriastrum densifolium, Cryptantha clevelandei, Mimulus aurantiacus, Hemizonia* sp., *Achillea millefolium, Stephanomeria virgata, Bromus rubens, Festuca megalura, Bromus mollis, Avena fatua*, and *Eremocarpus setigerus* (Fitch, 1948; A. I. Roest, in litt.; Tappe, 1941). Additionally, seeds of the following plants have been found in the burrows of these kangaroo rats: *Avena fatua, Bromus mollis, B. rubens, Calindrinia caulescens, Eriogonum* sp., *Erodium cicutarium, Lotus* sp., *Lupinus* sp., and *Trifolium* sp. Plant material other than seed include: *Atriplex* sp., *Avena fatua, Bromus rubens, Eriogonum angulorum, E. fasciculatum, Erodium* sp., *Euphorbia serpyllifolia, Gutierrezia californica, Juniperus californicus, Lastarriaea chilensis, Lepidum nitidum*, and unidentified heads of Compositae (Fitch, 1948). Cheek pouches in summer yield an abundance of plant species, the most frequent of which are *Bromus mollis, Festuca megalura*, and *Erodium* sp. (Fitch, 1948).

Seeds are the most nutritionally important part of the diet of this species, although green vegetation composes a large part of the diet as well, especially in winter and spring (Tappe, 1941). Most seeds are returned to the burrow, whereas nearly all succulent material is eaten outside the burrow. About 70% of the plant species growing near the burrows are utilized. Approximately 75% of these are grasses; the remainder are forbs. Only small food stores are found in burrows (the largest was 157 g); these are in pockets in the walls of the tunnels or at blind ends (Tappe, 1941). Early in the season, *Erodium* is used more heavily. During the dry season, *Bromus mollis* is the major food item, although *Erodium, Bromus rubens*, and *Festuca megalura* also are used commonly (Fitch, 1948). Seeds of these and of *Avena fatua* occur in large quantities in burrows (Tappe, 1941). *Eremocarpus setigerus* frequently is fed upon during fall, and in winter the diet changes to green foliage, with *Erodium* again dominating. Pine nuts (*Pinus sabiniana*) also are gathered, although in small quantities (Fitch, 1948). *D. heermanni* uses refuse piles of the black harvester ant (*Veromessor pergandei*) as a source of seeds. Wild kangaroo rats will capture insects at night, including moths (Lepidoptera), beetles (Coleoptera), and grasshoppers (Gryllacrididae); caged specimens catch and eat moths and beetles (Tappe, 1941). Although Tappe (1941) thought that insects probably were a considerable part of the diet of this kangaroo rat, Stewart and Roest (1960) reported plant foods to be selected over insects.

Heermann's kangaroo rat is incapable of supplying its entire water requirements with water produced metabolically (Nichters, 1957; Tappe, 1941). However, they apparently meet their water balance with water obtained from their food or from dew, although they may use puddles of rainwater (Tappe, 1941). Individuals caged for 2 weeks with neither water or moist foot will take water from a pan (Tappe, 1941). However, rather than drink directly from the pan they will lick water from their paws after skimming them over the water surface. Standard water bottles with tubes also are used by caged animals.

Under imposed conditions of dry food and low humidity, the mean-daily activity of *D. heermanni* drops considerably from that maintained when fed dry food at moderate humidity. Under the latter conditions activity patterns are erratic with respect to water consumption. Overall, no definite trend is exhibited (Nichters, 1957).

Rodents associated with *D. heermanni* include *Ammospermophilus nelsoni, Dipodomys ingens, D. nitratoides, Onychomys torridus, Perognathus californicus, P. inornatus, Peromyscus boylei, P. californicus, P. truei, Reithrodontomys megalotis*, and *Spermophilus beecheyi* (Culberson, 1946; Hawbecker, 1943, 1951; Quast, 1954; Stewart and Roest, 1960; Tappe, 1941). Where Heermann's kangaroo rat populations are high, these syntopic rodents usually are uncommon. The converse is also true. The social dominance of kangaroo rats, competitive superiority, or both, may cause this pattern (G. R. Stewart, in litt.).

The following fleas (including their frequency of occurrence, where available) have been reported: *Monopsyllus wagneri* (0.04), *Malaraeus telchinum* (0.07), *Thrassis aridus* (0.14), *Meringes cummingi* (0.86), and *M. parkeri* (Coultrip et al., 1973; Hardy et al., 1974*b*). An average of 3.1 fleas (all species) per kangaroo rat was reported from Kern Co. (Coultrip et al., 1973). Of 52 Heermann's kangaroo rats examined in San Luis Obispo Co., fleas were found on 38, lice on 19, and ticks on 18 (Stewart and Roest, 1960). Ticks include *Dermacentor parumapertus, Dermacentor* sp., and *Ixodes* sp. (Coultrip et al., 1973; Hardy et al., 1974*b*).

Endoparasites include the cestodes, *Hymenolepis citelli* and *Catenotaenia linsdalei* (King and Babero, 1974). The coccidium *Eimeria mojavensis* can be successfully introduced into *D. heermanni*, although it has not been found in natural populations. *D. heermanni* was the least susceptible of 10 rodent species investigated for this parasite (Doran, 1953). A Heermann's kangaroo rat from Madera Co. contained one trophozooite of *Giardia* in its blood (Herman, 1943). *D. heermanni* is not known to carry plague (Nelson, 1980), and is an aberrant host of western equine encephalitis (Hardy et al., 1974*a*). Fitch (1948) reported disease to be uncommon in specimens he examined.

Predators include rattlesnakes (*Crotalus viridis*), gopher snakes (*Pituophis melanoleucus*), owls (*Tyto alba* and *Bubo virginianus*), various raptors, coyotes (*Canis latrans*), foxes (*Urocyon cinereoargenteus* and *Vulpes macrotus*), weasels (*Mustela frenata*), skunks (*Mephitis mephitis*), and house cats (*Felis catus*; Childs, 1952; Fitch, 1948; Grinnell et al., 1930; Hawbecker, 1953; A. I. Roest, in litt.; Tappe, 1941). Predation evidently is not a significant determinant of population densities, because populations fluctuate markedly in years of stable predator populations (Fitch, 1948). During times with low populations of kangaroo rats, predators may be instrumental in maintaining reduced numbers, but a more critical factor appears to be local climate (Fitch, 1948). During Fitch's (1948) 6-year study, long-term populations seemed to fluctuate inversely with levels of rainfall.

Annual consumption is approximately 1.8 kg of dry mass per animal (Fitch, 1948), although these kangaroo rats apparently destroy much more vegetation than they eat. The plant yield (dry mass) on an experimental plot (79 kangaroo rats/ha) was 13.1 to 15.5% less/ha than on a control plot, indicating destruction of approximately 5.3 kg/kangaroo rat during the 7-month growing season (Fitch, 1948). The loss primarily was caused by stunted plant growth resulting from cropping young shoots. In most areas however, this loss would be 3 to 25% of this amount because kangaroo rat population densities generally are lower elsewhere (Fitch, 1948).

BEHAVIOR. Kangaroo rats do not hibernate, but may be more or less active at any time of day throughout the year. *D. heermanni* primarily is nocturnal and spends approximately 23 h/day within the burrow. Under normal conditions, light intensity apparently is the primary factor regulating the time of emergence from their burrows. Their surface activity is greatest in the early part of the night; they usually emerge soon after dark. When the moon is full and shining brightly in the evening however, they will concentrate their activity after moonset. These kangaroo rats generally avoid above-ground activity on cold, wet, windy, or moonlit nights. Only fog and rain have been found to keep *D. heermanni* in their burrows (Tappe, 1941). Although some individuals forage all night, most have two periods of activity, the first lasting for about 40 min, after which they retire to their burrows for up to 4 h. They often re-emerge for variable lengths of time, after which they generally are inactive. Immature Heermann's kangaroo rats are less cautious and often forage in full moonlight (Tappe, 1941).

These kangaroo rats are solitary; captives usually fight with other individuals placed in their cages (Tappe, 1941). Females are less aggressive than males and sometimes become accustomed to others to the point of sharing the same nest without fighting. Nonetheless, they remain prone to aggression (Fitch, 1948).

Tappe (1941) heard no vocal sounds in any free-living rats at night. Caged specimens make low chuckles at intervals, but only when disturbed. Upon removal from traps occasionally they make a "plaintive, low pitched, rattling squeak" (Tappe, 1941:132). A similar squeak is made by females placed in a cage with a male during the breeding season (Tappe, 1941). The most commonly heard sound is a fluttering or rattling sound (Tappe, 1941) made by one (although possibly two) hind foot when repeatedly struck against the ground (Eisenberg, 1963). This is made just before they emerge from their burrow or when disturbed (Tappe, 1941).

Adults usually forage along surface runways, although they gather food at considerable distances to either side. Foraging is in all directions except when burrows are on steep hillsides; there, foraging is on or above the contour of the lowest burrow entrance (Tappe, 1941).

Dipodomys heermanni gleans most of its food from the ground, but when grasses are ripening most foraging consists of gathering seed heads by standing on their hind feet, holding a seed head with their forefeet, and snipping off the stem with their teeth. Seed heads are then stuffed in their cheek pouches for transport (Tappe, 1941).

As with other species of kangaroo rats, these animals have no special areas for defecation, but deposit droppings indiscriminately outside the burrow (Tappe, 1941). At ambient temperatures of 20°C, *D. heermanni* sleeps in a quiet crouch with its head tucked between its feet. At thermoneutral temperatures (30°C) they sleep in more open postures, on their sides, and sometimes on their backs (Sakaguchi et al., 1979).

Captive *D. heermanni* rarely show sexual behavior when placed together, even when the female is in breeding condition. Captive matings are preceded by the male following the female around the cage for several minutes nosing her genitalia in apparent excitement. Females with enlarged and swollen genitalia are hostile and unreceptive; those that mate are recently perforate (Fitch, 1948). Copulation in captive animals requires only a few seconds (A. I. Roest, in litt.).

Labor is accompanied by a series of abdominal contractions each lasting about 3 s and consisting of six to eight contractions. Groups are separated by about 40 s. During parturition, the female sits hunched on her hind feet and aids the birth by pulling at the infant when it is partially emerged. When birth is complete, the mother turns to the young, smells it, licks it, and fondles it with her forepaws (Tappe, 1941). In moving its young, the mother usually picks up the infant by the back with her mouth. She further supports the infant by holding her front paws under its belly, then moves by hopping (Tappe, 1941).

Burrows of this species usually have one to four escape tunnels in addition to the main entrance. They may break through the thin crust separating some tunnels from the surface to elude predators in their burrow. If pursued on the surface they dart into the most available hole, or if none is available or if exhausted they may take refuge under a bush or "freeze," whereby they lay outstretched and motionless except for panting and wiggling of the vibrissae (Tappe, 1941).

Heermann's kangaroo rats usually dust-bathe after foraging. When bathing, they keep either the foreparts or hind parts upright, sometimes lying on their bellies with both hind legs stretched out. Bathing apparently removes oil and moisture, and keeps their hair dry and sleek. Fur of caged individuals that cannot bathe becomes matted, especially around the dermal gland (Tappe, 1941).

These animals often use paths of other animals, roads, firebreaks, and other trails. Locomotion generally is bipedal. Slow movement over short distances often is plantigrade and may be quadupedal with the tail either dragged loosely behind or held slightly off the ground. In slow bipedal movement (about 0.76 m/s) these animals usually hold their tails straight with the distal one-third bent upward, and proceed by a series of quick hops, each about 15 cm long. Moderate and rapid movement usually is saltatorial, and fast movement often is ricochetal. In rapid running, hops are longer (usually <61 cm, but up to 76 cm), and the tail is used as a counterbalance (Tappe, 1941). When clocked for speed, *D. heermanni* demonstrate a daytime maximum of 5 m/s, and a nightime maximum of 5.4 m/s. Although endurance decreases under strenuous exertion, it is high during routine activities.

GENETICS. Based on 49 specimens collected from three populations Johnson and Selander (1971) reported minor geographic variation in allele frequencies at 17 loci. They concluded that the degree of genetic variability was similar to that of other species of *Dipodomys*. The frequency of polymorphic loci per population was 0.17; the frequency of heterozygous loci per individual was 0.042. Although these values are low for rodents in general, they are among the highest recorded for the genus (Johnson and Selander, 1971). Patton et al. (1976) analyzed 30 individuals from three populations and found similar numbers of alleles per locus ($\bar{X} = 1.17$ and 1.22, for two populations with more than one representative) and similar allele frequencies at polymorphic loci. The proportion of loci heterozygous per individual also was close to Johnson and Selander's (1971) value ($H = 0.037$ and 0.035), whereas the proportion of polymorphic loci per population was somewhat lower ($P = 0.05$ and 0.09). Of the proteins studied, isocitrate dehydrogenase-2, α-glycerophosphate dehydrogenase-1, 6-phosphogluconate dehydrogenase-1, glutamate oxalate transaminase-1, sorbitol dehydrogenase, and xanthine dehydrogenase showed little geographic variation (Johnson and Selander, 1971; Patton et al., 1976).

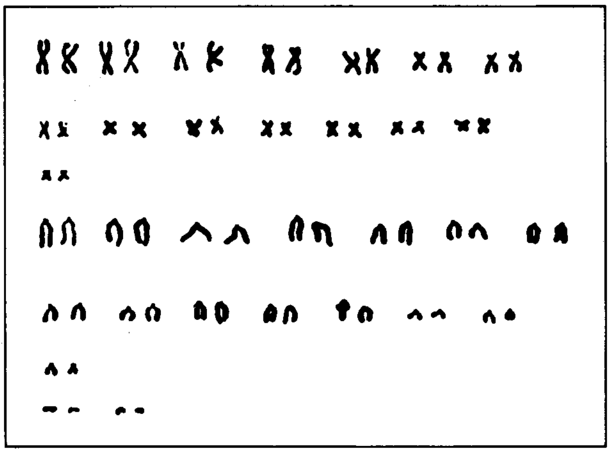

FIG. 4. Karyotype of an adult female *Dipodomys heermanni goldmani* from 2.5 mi W Little Pinnacle Ranger Station, Pinnacles National Monument, San Benito Co., California. Specimen from the Los Angeles County Museum of Natural History (TK 182), courtesy of B. A. Csuti.

Dipodomys heermanni has a diploid number of 64 (fn = 90), with 28 to 32 metacentric and 30 to 34 acrocentric autosomes (Fig. 4). The X-chromosome is metacentric, and the Y-chromosome is either metacentric or acrocentric (Csuti, 1971; Stock, 1971, 1974).

Johnson and Selander (1971) and Patton et al. (1976) demonstrated close genetic similarity between *D. panamintinus* and *D. heermanni* (Roger's coefficient of genetic similarity, $S = 0.89$ and 0.925 for these two studies, respectively), with *D. microps* and *D. agilis* also similar. This agrees with Stock's (1971, 1974) karyological treatment of this genus in allying *D. microps* with these species. Although *D. californicus* was long considered synonymous with *D. heermanni*, Patton et al. (1976) showed that these species are genetically more distinct from each other ($S = 0.787$) than either is from *D. panamintinus* ($S = 0.859$ and 0.925, respectively). Although Johnson and Selander (1971) did not consider *D. ingens*, it generally is considered closely related to *D. heermanni* (Grinnell, 1922; Lidicker, 1960*a*; Setzer, 1949; Stock, 1971, 1974). Stock (1974) believed that *D. ingens* and *D. panamintinus* were derived from *D. heermanni*, which in turn shared ancestral stock with *D. stephensi* and *D. gravipes*. On the basis of karyological similarity, Stock (1974) implied that *D. californicus* may be more closely related to *D. nitratoides* of the *merriami* group. This been considered convergence by Patton et al. (1976) who used electrophoretic separation of proteins to show *D. californicus* to be more closely allied with *D. panamintinus* and *D. heermanni* ($S = 0.859$ and 0.787, respectively) than to *D. nitratoides* ($S = 0.502$). Clearly, further work is needed before actual relations of *D. heermanni* with its congeners can be clarified. However, it should be recognized that demonstration of affinities among species of *Dipodomys* is complicated by morphological convergence and relatively low genetic variability within the genus, and the lack of association between phenetic groups based on such data (Schnell et al., 1978).

Dipodomys heermanni has the following DNA composition: principal DNA (1.698 g ml^{-1} s^{-1}), 44%; intermediate DNA (1.702 g ml^{-1} l^{-1}), 23%; medium density satellite DNA (1.707 g ml^{-1} l^{-1}), 19%; heavy density satellite DNA (1.713 g ml^{-1} l^{-1}), 14% (Mazrimas and Hatch, 1972).

REMARKS. The Morro Bay kangaroo rat (*D. h. morroensis*) was listed as endangered by the federal government in 1970 (Federal Register, 35(199):16047), and by the state of California in 1971, and is listed as endangered by the International Union for Conservation of Nature and Natural Resources (1982). Populations of this subspecies have declined by more than 80% in the past 20 years because of loss of suitable habitat (A. I. Roest, in litt.) through direct human encroachment and lack of natural disturbance by fire or other factors for over 30 years. Absence of such disturbance has resulted in a maturation of the flora to a type that is much less suitable for the species. The limited range is subdivided into several smaller parcels that are isolated from each other by distances of 2 km or more, reducing interpopulation movements considerably. Although efforts are being made to protect and preserve suitable habitat, the probability of full recovery seems remote for this subspecies (A. I. Roest, in litt.).

Dipodomys is from the Greek *di*, meaning two, *podo*, meaning foot, and *mys*, meaning mouse. The specific epithet honors Dr. Adolphus L. Heermann, the collector of the type specimen.

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