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Dipodomys californicus.

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Dipodomys californicus Merriam, 1890

California Kangaroo Rat

Dipodomys californicus Merriam, 1890:49. Type locality "Ukiah, Mendocino County, California."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Dipodomyinae. Three subspecies of *Dipodomys californicus* currently are recognized (Patton et al., 1976) as follows:

D. c. californicus Merriam, 1890:49, see above (*pallidulus* Bangs, *trinitatis* Kellogg, and *gabrielsoni* Goldman are synonyms).

D. c. eximius Grinnell, 1919:205. Type locality "Marysville Buttes at 300 feet altitude, 3 miles northwest of Sutter, Sutter County, California."

D. c. saxatilis Grinnell and Linsdale, 1929:453. Type locality "mesa near Dale's, on north side of Paine's Creek, 700 feet altitude, Tehama County, California."

DIAGNOSIS. *Dipodomys californicus* is a medium-sized kangaroo rat (Fig. 1). It is a "broad-faced" species (Grinnell, 1922) with a prominent and sharp posteroexternal angle of the maxillary arches (Fig. 2); breadth of maxillary roots is greater than 54.8% of the greatest length of the skull (Hall, 1981). Where *D. californicus* evidently is sympatric with *D. deserti* and *D. merriami* (James and James, 1984), it may be distinguished by its darker coloration and by size. *D. californicus* is intermediate in weight and external measurements, especially hindfoot length, between the smaller *D. merriami* and the larger *D. deserti* (Grinnell, 1922; Hall, 1981). Additionally, both *D. deserti* and *D. merriami* are narrow-faced kangaroo rats (Grinnell, 1922). Southern members of *D. californicus* closely resemble some northern members of *D. heermanni* in external appearance and cranial features. The former can usually be distinguished by the absence of the hallux or by the presence of a distinct white tip on the tail (Grinnell, 1922; Grinnell and Linsdale, 1929).

GENERAL CHARACTERS. The general pattern of pelage coloration is consistent throughout the genus (Hall, 1981). Pelage in *D. californicus* is silky throughout. The dorsal guard hairs are unbanded, taper abruptly, and possess well-developed medullary aggregations located in individual invaginations in the medullary substance. These hairs usually are 13 mm or less in length (if 13 mm, then medullary aggregations are not more than three abreast), and cortical pigmentation is prominent for <4 mm along the length of the shaft. An exception is *D. c. californicus*, in which dorsal guard hairs have a maximum length of 15 mm and width to 45 μm; the distal fraction of a millimeter possesses dark medullary (not cortical) pigmentation, which is subtended by a 2 mm black band (Mayer, 1952). External measurements (in mm) are: total length, 260 to 340; length of tail, 152 to 217; length of hind foot, 40 to 47; length of ear, 11 to 16 (Grinnell, 1922; Grinnell and Linsdale, 1929). Means of selected cranial measurements (in mm; males and females, respectively) are (Best, in press): greatest length, 38.9, 38.7; basal length, 22.4, 22.3; nasal length, 15.0, 14.9; maxillary arch spread, 22.6, 22.6; interorbital width, 10.8, 10.7; maxillary arch width, 5.5, 5.5; greatest depth, 12.9, 12.9; greatest width, 23.6, 23.5; zygomatic width, 20.2, 20.1. Means of all skull and external measurements showed slight sexual dimorphism, with males larger in most of them (Best, in press; Dale, 1939); a large amount of variation exists however, in measurements of specimens selected for uniform age and sex (Dale, 1939), and using 191 adult males and 150 adult females, Best (in press) found only tail length, alveolar length, and nasal width to be significantly dimorphic.

DISTRIBUTION. This species is found in south-central Oregon and northern California, north of a line roughly extending between Suisun Bay and Lake Tahoe, California, and chiefly east of the humid coastal regions to the foothills of the Cascade and Sierra Nevada mountains (Fig. 3; Grinnell, 1922; Hall, 1981). *D. californicus* is not known from the fossil record.

FORM AND FUNCTION. As all members of the genus, *D. californicus* possesses expanded auditory bullae, a light, papery skull, reduced forelimbs, powerful hindlimbs, a long, tufted tail, and external, eversible, fur-lined cheek pouches. The dorsal body surface in this species ranges from tawny-olive strongly overwashed with black (*D. c. californicus*) to various shades of cinnamon-buff and pinkish-buff extensively obscured (*D. c. eximius*). The tip of the tail usually is crested (Grinnell, 1922; Grinnell et al., 1930).

Dipodomys californicus possesses two pairs of inguinal mammae and one pair of pectoral mammae (Bailey, 1936). The dorsal skin gland in *D. californicus* secretes year-round in 90% of adults, with no significant sexual dimorphism and little seasonal variation in glandular activity. Level of gland activity is not related to the 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). Although the upper premolars in the original members of this family probably were quadritubercular (Wood, 1935), in this species these teeth appear to display six cusps, arranged as an anterior cusp followed posteriorly by two transverse rows of cusps, the first row bearing two cusps, the second row with three cusps; between these rows is an enamel covered valley that deepens bucally (Dale, 1939). In the third molar the cusps are never complete, but are merged into transverse troughs without a complete roofing of enamel. Cusps on both premolars and molars begin to wear at an early age (Dale, 1939).

ONTOGENY AND REPRODUCTION. Breeding primarily occurs from February through September (Bailey, 1936; Dale, 1939; Grinnell et al., 1930), with greatest activity in February, March, and April. This species apparently is capable of producing more than one litter annually (Dale, 1939). In Tehama Co., California, Dale (1939) found an overall average embryo count of 2.7 (n = 20; range, 2 to 4), with an average of 3.1 (n = 11) for spring and 2.1 (n = 9) for the remainder of the year.

Skulls may be placed into relative age groups on the basis of tooth development and cheektooth wear as follows (Dale, 1939): juvenile skulls retain the deciduous premolar, which is relatively unworn; young skulls are those in which the premolar is not yet at the level of the molars, but milk teeth, if present, are well worn; subadult skulls, from animals 3 to 5 months old, with adult pelage,

FIG. 1. Adult California kangaroo rat (*D. c. californicus*), from Lava Beds National Monument, Modoc Co., California. Photograph courtesy of S. B. Cross.

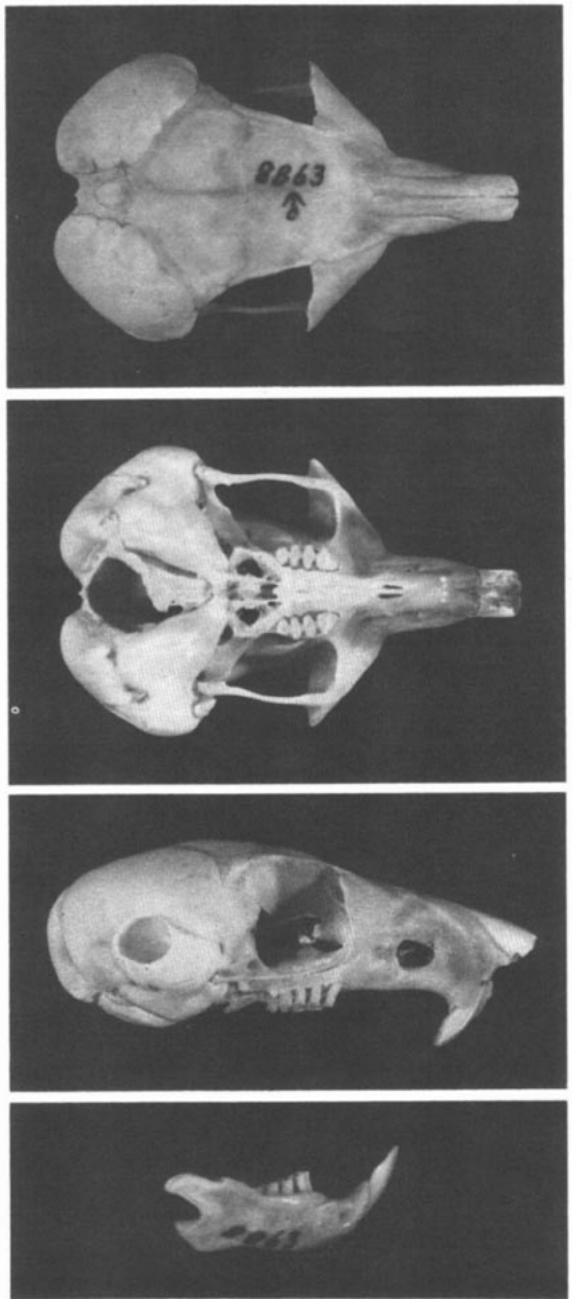

FIG. 2. Dorsal, ventral, and lateral views of the cranium, and a lateral view of the mandible of an adult female *Dipodomys californicus californicus* (Field Museum of Natural History 8863) from Nicasio, Marin Co., California. Greatest length of skull is 35.2 mm. Photographs by C. Garner.

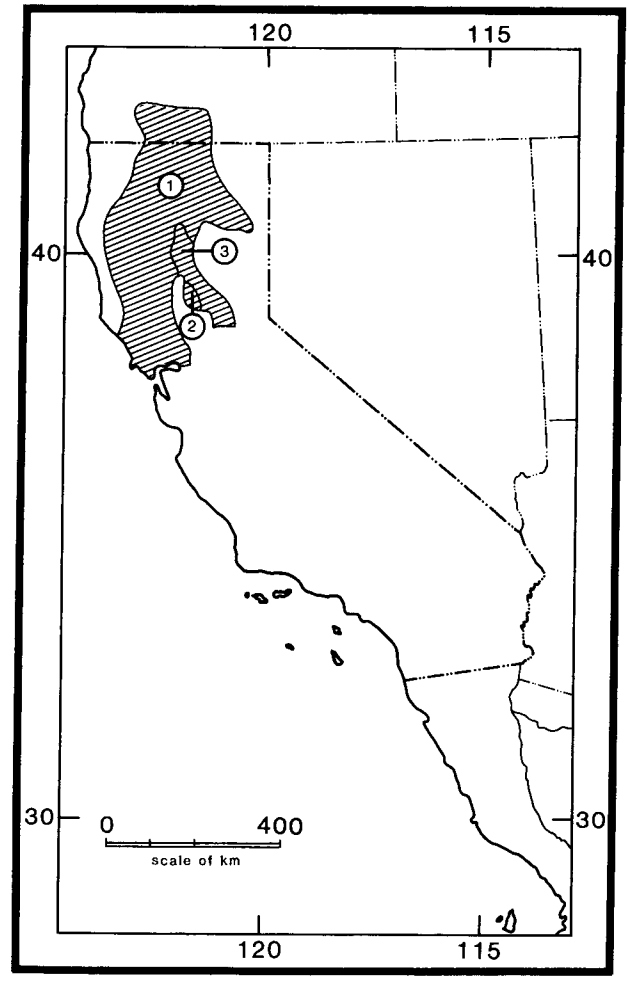

FIG. 3. Distribution of *Dipodomys californicus*. Subspecies boundaries from Hall (1981): 1, *D. c. californicus*; 2, *D. c. saxatilis*; 3, *D. c. eximius*. Figure prepared by C. Garner.

and nearly as large as adults, differ from adults in the lesser degree of wear on the cheekteeth; in adults the cheekteeth are well worn. Juvenile skulls are characterized by rough, pitted bone, which is replaced by firmer and smoother bone throughout growth. These skulls are short (approximately 87% of adult length), relatively broad, and highly arched on the dorsal surface. Ossification begins on the ventral side of the auditory bullae, dorsal side of nasals, rostral part of maxillary and premaxillary, and in four locations on the dorsal cranium, one in each of the parietal and frontal bones. The last parts of the skull to ossify evidently are the mastoidal bullae and zygomatic part of the maxillary. In young skulls, the length of the skull has increased more than bullar breadth, maxillary arches have become relatively and actually wider as compared to length and to mastoidal breadth, the nasals have increased more rapidly than the skull, and the dorsal surface is less strongly arched. Subadult skulls increase relatively little in size, with more increase in length than breadth, and the greatest increase in the maxillary part of the skull, all relative to the young condition. Adult skulls are only slightly larger than subadults, the nasals are relatively and actually a little longer, and the maxillary arches are considerably broader (Dale, 1939).

ECOLOGY. The ecological distribution of *D. californicus* seems to be limited to some degree by moisture and other factors associated with moisture (Dale, 1939). This species occupies habitats predominantly in the Upper Sonoran life zone, but extends well into the Lower Sonoran and locally into the Transition life zone (Grinnell, 1922). These rodents are not found in lush vegetation, and while tolerant of regions of "hard chaparral" (represented principally by *Ceanothus cuneatus*), they appear to be restricted to places where open areas are available (Dale, 1939). *D. californicus* generally requires well-drained soils throughout the winter (Grinnell and Linsdale, 1929), although they have been reported to dig burrows in hard clay or gravelly soils (Bailey, 1936; Grinnell et al., 1930) and in rocky areas with thin soil (Dale, 1939). In chaparral areas, these kangaroo rats make their burrows at the bases of shrubs and around old stumps (Bailey, 1936). In areas unsuitable for burrowing, they usually excavate homes under large boulders (Dale, 1939; Grinnell et al., 1930). *D. californicus* also uses burrows of ground squirrels (*Spermophilus*; Grinnell et al., 1930).

Plants growing on hard-packed slopes often inhabited by *D. californicus* generally produce a greater ratio of seed to stem than plants in bottomlands within its range. Where these animals are abundant, many fecal pellets usually are found along trails and especially at dusting areas. Fecal pellets are 5 to 6 by 2 to 3 mm, tapered at both ends, slightly curved, and black (Dale, 1939).

In a study area dominated by ceanothus (*Ceanothus velutinus* and *C. prostratus*), manzanita (*Arctostaphylos patula*), wild cherries and plums (*Prunus* spp.), and serviceberry (*Amelanchier alnifolia*), seeds and berries of manzanita were found to be the staple food of *D. californicus* during fall (Smith, 1942). Bailey (1936) found cheek pouches to contain berries and seeds of manzanita, seeds of buckbrush (*Ceanothus cuneatus*), rabbitbrush (*Chrysothamnus* sp.), lupines (*Lupinus* sp.), bur-clover (*Medicago* sp.), wild oats (*Avena barbata*), and some small tubers. Green vegetation apparently is selected in spring (Dale, 1939). Cheek pouches of animals caught in the summer contain green vegetation (Grinnell et al., 1930). Although consumption of green vegetation at this season may be necessitated by depletion of seed stores laid away the preceding summer, difficulty in trapping *D. californicus* with dry bait at this season indicates that this representation may be due to selection. Dry seeds again dominate the diet between May and December (Dale, 1939). That *D. californicus* does not maintain large food stores has been attributed to seed caches being deposited randomly in the soil a cheekful at a time (Dale, 1939).

The following fleas (with their frequency of occurrence where available) have been reported: *Monopsyllus eumopli* (0.01), *Opisidasys keeni* (0.01; Stark and Kinney, 1969), *Meringes cummingi* (0.56 and 0.10; Hubbard, 1961*a*, and Stark and Kinney, 1969, respectively), and *M. parkeri* (0.07; Stark and Kinney, 1969). From nine California kangaroo rats, Hubbard (1961*b*) found 216 (n = 10; range, 0 to 12) fleas in October, whereas Stark and Kinney (1969) found only 0.3 fleas per individual during March and April, and none on 24 *D. californicus* examined during May and June. The only tick reported for this species is *Rhipicephalus sanguineus* (Enright et al., 1971). Dusting probably removes parasites (Dale, 1939) and has been postulated to remove fats and oils from the pelage (Howell, 1932).

The rickettsia (*Coxiella burnetti*, causative agent of Q-fever, is known from *D. californicus*, although this kangaroo rat showed the lowest prevalence of antibody against Q-fever of 21 rodent species analyzed during a three-year study (Enright et al., 1971). Carcasses of *D. californicus* were found in an area where a Belding ground squirrel (*Spermophilus beldingi*) plague epizootic was occurring; no specimens of *D. californicus* were tested however (Meyer, 1947). In contrast, Nelson (1980) found no carcasses or evidence of die-offs in any population of *D. californicus* in areas where plague epizootics were in progress.

Natural enemies include foxes (*Urocyon cinereoargenteus* and *Vulpes* sp.), coyotes (*Canis latrans*), owls (Tytonidae and Strigidae), and snakes (Squamata; Bailey, 1936). During times when *D. californicus* populations are low, predators may be instrumental in maintaining reduced numbers, but local climate evidently is a more significant factor regulating populations (Dale, 1939).

BEHAVIOR. *Dipodomys californicus* do not hibernate and are nocturnal, becoming active soon after dark. Although wet weather is considered to be the principal cause of decimation of populations during severe winters, this species is surprisingly tolerant of moist conditions and may be active on rainy nights, although generally less so than on nights without precipitation. After heavy rains these animals will clean mud out of their burrows (Dale, 1939). These animals may be active on snow and in temperatures as low as −11°C (Dale, 1939; Grinnell et al., 1930).

Dipodomys californicus often uses paths of other animals, roads, firebreaks, and other trails. Movement in this species generally is bipedal, and most often is semidigitigrade. Unlike some other species of kangaroo rats, *D. californicus* evidently does not make long leaps when excited, but rather appears to "scamper" at such times (Dale, 1939).

GENETICS. *Dipodomys californicus* has a diploid number of 52 (fn = 96); 46 autosomes are metacentric, and 4 are acrocentric. Both sex chromosomes are metacentric (Fashing, 1973). Stock (1974) noted that *D. californicus* was karyologically more similar to *D. nitratoides* of the *merriami* group than to *D. heermanni*, inferring a possible relationship, but this was considered convergence by Patton et al. (1976), who showed *D. californicus* to be allied more closely to *D. heermanni* on the basis of allozyme complements; this latter interpretation has been corroborated by phenetic analyses (Best, in press; Schnell et al., 1978). Starch gel electrophoresis revealed little geographic variation in isozymes of *D. californicus* among 33 individuals from two populations (Patton et al., 1976).

REMARKS. On the basis of bacular morphology and the degree of karyotypic reorganization, Stock (1974) divided the *heermanni* group into five subgroups, one of which contains *D. ingens*, *D. panamintinus*, and *D. heermanni* (including *D. californicus*). The instability of hind-toe characters in *Dipodomys* led Grinnell (1922) to synonymize *D. californicus* (four-toed) with *D. heermanni* (five-toed). On the basis of significant genic and genetic differences between the northern (four-toed) and southern (five-toed) populations however, Patton et al. (1976) suggested that the northern taxa should be specifically recognized as *D. californicus*. Although data are unavailable for *D. c. eximius*, they (Patton et al., 1976) believed that it "most likely should be arranged with this group [*D. californicus*] as well."

Dipodomys is from the Greek *di*, meaning two, *podo*, meaning foot, and *mys*, in reference to mouse. The name *californicus* refers to the state of California.

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