

*Dipodomys panamintinus*. By Clare Intress and Troy L. Best

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*Dipodomys panamintinus* (Merriam, 1894)  
Panamint Kangaroo Rat

*Perodipus panamintinus* Merriam, 1894:114. Type locality "Panamint Mts. [Inyo Co.], California (on head of Willow Creek)."

*Perodipus mohavensis* Grinnell, 1918:428. Type locality "3275 feet altitude, half mile east of railway station of Warren (about five miles north of Mohave), Kern County, California."

*Perodipus leucogenys* Grinnell, 1919:46. Type locality "5600 feet altitude, Pellisier Ranch, five miles north of Benton Station, Mono County, California."

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

**CONTEXT AND CONTENT.** Order Rodentia, Family Heteromyidae, Subfamily Dipodomysinae. The species contains five subspecies (Hall, 1981):

*D. p. argusensis* Huey, 1945:131. Type locality "Junction Ranch, 5725 feet altitude, Argus Mountains, Inyo County, California."

*D. p. caudatus* Hall, 1946:409. Type locality "6 mi. S Granite Well, 3800 feet, Providence Mountains, San Bernardino County, California."

*D. p. leucogenys* (Grinnell, 1919:46), see above.

*D. p. mohavensis* (Grinnell, 1918:428), see above.

*D. p. panamintinus* (Merriam, 1894:114), see above.

**DIAGNOSIS.** Several congeners occur sympatrically or near the range of *D. panamintinus*. *D. stephensi* has hind feet that usually are less than 42.5 mm in length, a tail that is 145-154% of the length of head and body, a white tail stripe about one-half as wide as the dorsal stripe, and a dark ventral tail stripe that extends to the end of the caudal vertebrae (Ingles, 1965). *D. agilis* has much larger ears, darker coloration (Grinnell, 1922), a tail that is about 155% of the length of the head and body, and a white tail stripe almost as wide as the dorsal tail stripe at mid-tail. *D. heermanni* has a tail that is about 150% of the length of the head and body; the tail is light gray or whitish, tipped with little or no crest. *D. merriami* is smaller and has four toes on its hind feet. *D. microps* has flattened incisors that usually are wider than 1 mm. *D. ordii* is smaller, has a tail that is 120-130% of the length of head and body, has a white tail stripe that is as wide as or wider than the ventral dark tail stripe, and the ventral tail stripe never reaches the end of the vertebrae (Ingles, 1965).

**GENERAL CHARACTERS.** The Panamint kangaroo rat (Fig. 1) is medium-sized for the genus (Best, in press). Morphologically, it is adapted for ricochetal locomotion (Eisenberg, 1963). The hind foot has five toes. The tail is heavily crested and amounts to about 140% of the length of the head and body, or about 58% of the total length (Hall, 1946), and has a ventral stripe that may extend to the end of the vertebrae (Ingles, 1965).

The upper parts are pale buffy clay-color, tinged with pale ochraceous. Thigh patches are large, colored similar to the back. Facial crescents and end of nose are broadly blackish, but barely or not continuous over sides of nose; inner sides of legs are dusky. Dorsal and ventral tail stripes are pale dusky, the ventral stripe failing or indistinctly continuous on distal third, permitting the lateral white stripes to meet below on distal third. Eyelids and anterior part (>50%) of reflexed upper border of ear blackish; posterior part of ear whitish (Merriam, 1894).

The interparietal is composed of a variable number of bones (Fig. 2); there is one bone present in 85.1%, two bones in 5.5%, and no interparietal in 9.5% of specimens (Beer, 1965). The maxillary arch has a prominent rounded angle (Ingles, 1965). The evergrowing molariform teeth have an opening at the base of the root that is oval-shaped (Nader, 1966).

Mean measurements (in mm) of 467 adult males and 385 adult females, respectively, from throughout the range of the species are: total length, 292.4 and 287.8; length of body, 120.2 and 121.1; length of tail, 172.3 and 169.6; length of hind foot, 44.5 and 43.8; length of ear, 14.0 and 13.9; basal length of cranium, 22.7 and 22.5; greatest length of cranium, 39.9 and 39.4; maxillary arch spread, 23.1 and 22.8; interorbital width, 11.5 and 11.5; nasal length, 15.5 and 15.2; intermaxillary width, 7.8 and 7.7; alveolar length, 5.3 and 5.2; lacrimal length, 4.2 and 4.2; maxillary arch width, 5.4 and 5.3; basioccipital length, 5.7 and 5.6; greatest depth of cranium, 13.1 and 12.9; greatest width of cranium, 24.3 and 24.0; zygomatic width, 20.6 and 20.3; and nasal width, 4.0 and 3.9 (Best, in press). Mean body mass is about 72.4 g (Hafner, 1977).

Males average more than 2% larger than females in linear measurements, and about 14% heavier in mass (Hall, 1946). Males generally are larger and more variable than females (Harvey, 1972). Of 19 morphologic characters, 14 exhibit significant sexual dimorphism in size. Males are significantly larger in the 14 characters, including total length, length of tail, length of hind foot, greatest length of cranium, maxillary arch spread, nasal length, greatest depth of cranium, and greatest width of cranium (Best, in press).

**DISTRIBUTION.** *Dipodomys panamintinus* occurs in eastern California and western Nevada (Fig. 3; Hall, 1981). *D. p. leucogenys* and *D. p. mohavensis* have a continuous distribution. *D. p. argusensis* and *D. p. panamintinus* probably do not have contact with any other subspecies, but it is likely they have had recent contact with *D. p. leucogenys* and *D. p. mohavensis*. *D. p. caudatus* is isolated from the other subspecies by extremely arid desert (Dingman et al., 1971).

**FOSSIL RECORD.** No fossils of this species are known. At least by the early to middle Pleistocene, the presumed ancestors of *D. panamintinus* penetrated the Colorado and Mojave deserts and later spread throughout the Great Basin, California, and Baja California (Stock, 1974). *D. panamintinus* and *D. stephensi* may have diverged from a common ancestor during the middle Pleistocene (Setzer, 1949).

**FORM AND FUNCTION.** The fur is of silky texture; it is plumbeous basally on the upper parts, but white all the way to the base on the underparts. The tail, excepting its terminal fourth, and the ears, forefeet, and upper sides of the hind feet are short-haired (Hall, 1946). Mean length of hair is 12.6 mm (range, 12.1-13.1) and width is 0.03 mm; short to medium in length and medium in width for the genus. The base is wide; shaft and tip strait; tip tapers gradually. The cross section is oval; medulla cells are oval to flattened; cells are in regular rows of two or three cells across, alternating with one cell (Homan and Genoways, 1978). The distal 3 mm of

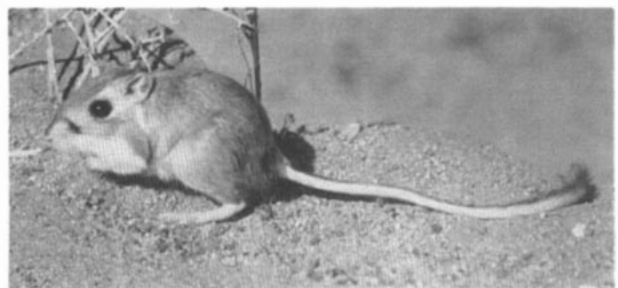


FIG. 1. *Dipodomys panamintinus* from near Pearlblossom, Los Angeles Co., California. Photograph by T. L. Best and S. B. George.

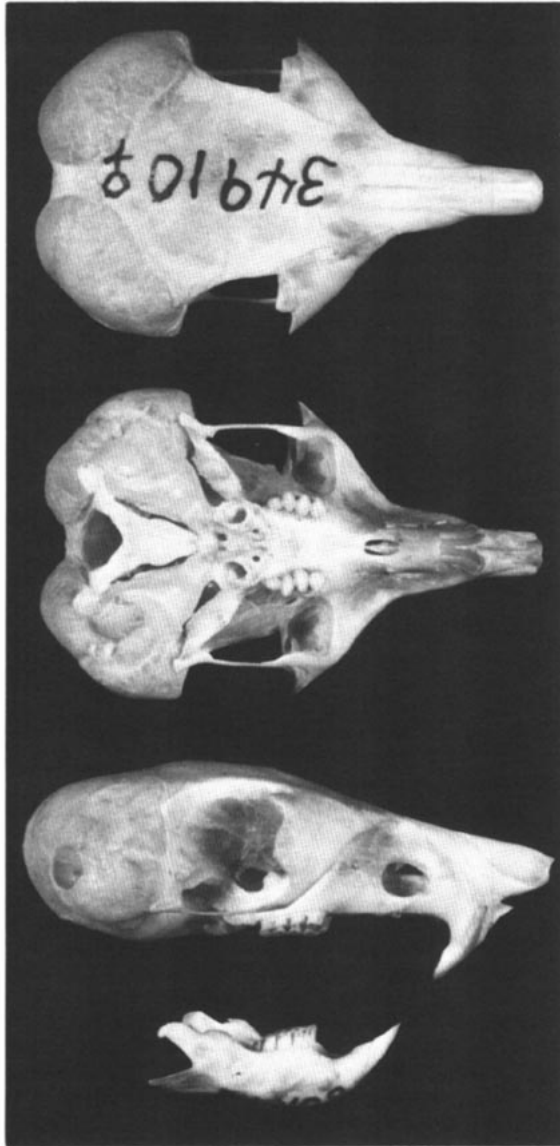


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Dipodomys panamintinus* (female from near Monolith, Kern Co., California, Museum of Southwestern Biology 34910). Greatest length of cranium is 38.7 mm. Photographs by J. L. Dobie and T. L. Best

dorsal guard hairs are darkly colored by cortical pigmentation (Mayer, 1952).

There is one molt per year. In Nevada, this molt usually occurs in June or July (Hall, 1946). In California, adults have old pelage in March, April, and May. The old pelage has an overall grizzly look and the fur is generally lighter and less shiny than freshly molted pelage found on animals in October and November. Juveniles molt from March through October (Harvey, 1972).

A holocrine skin gland is located mid-dorsally. It is an area of enlarged and modified sebaceous glands. Glandular area epidermis and dermis are thickened; elastic fibers, mast cells, capillaries, and melanophores are particularly abundant in the dermal partitions between gland units (Quay, 1954). Sebaceous and mucous glands are present at the oral lips and angle (Quay, 1965).

The baculum of *D. panamintinus* is indistinguishable from that of *D. heermanni* (Burt, 1960). Mean measurements (in mm) are: length, 10.38; height of base, 1.49; and width of base, 1.32 (Best and Schnell, 1974). The baculum has a nearly round base (dorso-ventral/lateral diameter of base) of 1.27, an index of robustness (dorso-ventral diameter of base + lateral diameter of base  $\times$  100/length) of 28.5, and a relative length (body length/baculum length) of 11.41 (Lidicker, 1960b).

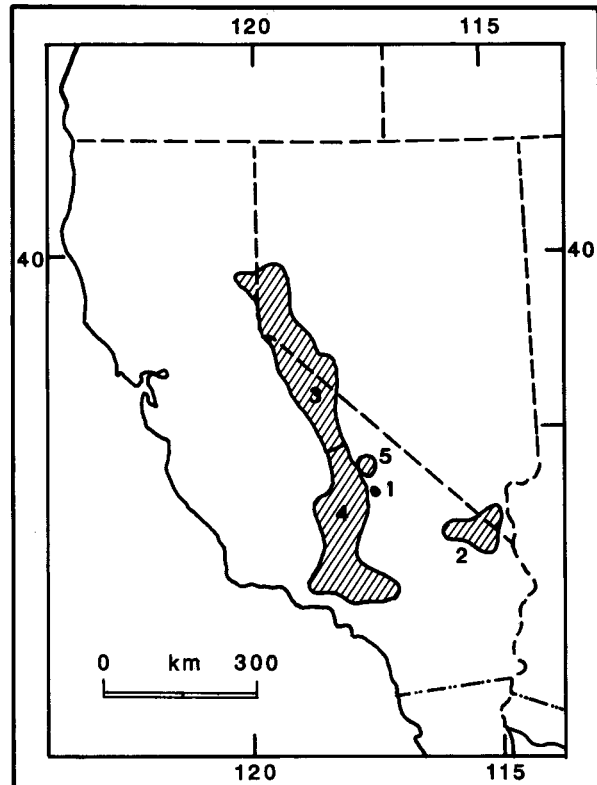


FIG. 3. Distribution of *Dipodomys panamintinus* in southwestern North America (Hall, 1981): 1, *D. p. argusensis*; 2, *D. p. caudatus*; 3, *D. p. leucogenys*; 4, *D. p. mohavensis*; 5, *D. p. panamintinus*.

Approximate volume of both cheek pouches is 3.4 ml (Lawhon and Hafner, 1981). The individual cheek pouch volume is 2.64 cm<sup>3</sup> (range, 2.33–2.95; Morton et al., 1980).

Skeletal indices include: humeroradial, 146.1; intermembral, 55.3; crural, 132.0; tibioradial, 57.5; femorotarsal–metatarsal, 90.5; and cranial, 60.8. *D. panamintinus* has an average specialization (based upon skeletal and visceral measurements) of 3.1 on a scale of 1 to 11; it is one of the least specialized species in the genus. Visceral measurements (in mm) are: length of large intestine, 419; length of small intestine, 255; and percent of small to large intestine, 60.9 (Setzer, 1949).

*Dipodomys panamintinus* has small ears and small auditory bullae in comparison to other *Dipodomys* (Setzer, 1949). The middle ear has the following dimensions (in mm unless otherwise indicated): volume, 0.43 cm<sup>3</sup>; relative volume, 0.23 cm<sup>3</sup>; tympanic membrane diameter, 5.24; length of stapes footplate, 1.41; width of stapes footplate, 0.75; length of malleus, 3.02; and length of incus, 0.95 (Webster and Webster, 1975).

The total dorsal surface area of the brain is 179.4 mm<sup>2</sup>. Of this area, the cerebrum accounts for 74%, the cerebellum 21%, and the olfactory bulbs 5%. The endocranial volume is 1.54 cc (Hafner and Hafner, 1984).

For each kidney, mass is 295 mg, glomerular radius is 48.4  $\mu$ , number of glomeruli is 18,840, and total glomerular volume is 8.9 mm<sup>3</sup> (Rytand, 1938). The Panamint kangaroo rat is able to excrete urine that is concentrated to 3.28 M (Schmidt-Nielsen and Schmidt-Nielsen, 1952). When deprived of water, it produces only a small drop of urine every 1–2 h; an average of 0.20–0.27 g animal<sup>-1</sup> day<sup>-1</sup>. When water is provided, 2.08 g of urine is produced in 8 h. Blood urea of animals deprived of water is 0.083% and with water is 0.030%. Urine urea of animals deprived of water is 13.2–19.7% and with water is 1.43%. The elimination of poisonous body wastes by the kidneys is not necessarily more efficient than that of *Rattus* (Howell and Gersh, 1935).

When deprived of food for 5 days, *D. panamintinus* shows polydipsia (elevated drinking) and more than triples its average daily water intake. This species, which subsists on little free water, responds mainly to decreased extracellular volume as a thirst cue. Because

decreased vascular volume occurs during food deprivation, this species overdrinks (Vander Wee et al., 1975). When presented with vegetation, *D. panamintinus* consumes more water than *D. agilis* and *D. stephensi*. Although these species inhabit areas with different degrees of aridity, they show similar capacities to maintain body mass and to concentrate urine when deprived of water. Because *D. panamintinus* occurs in an area of low rainfall and xerophytic vegetation, a possible increased need for water prior to reproduction may necessitate a higher level of consumption of seasonally available succulent vegetation (Sork, 1978). A regression analysis of metabolic water production/evaporative water loss is 2.504 (0.957) at an ambient temperature of 20.7°C and a mean mass of 64.2 g (MacMillen and Hinds, 1983). The rate of evaporative water loss is 0.044 mg of water  $g^{-1} h^{-1} ^\circ C^{-1}$  (Scelza and Knoll, 1975).

When placed into a small cage, *D. panamintinus* that previously have been given water have a 30% initial increase in rate of respiration, whereas animals deprived of water do not show this initial increase. Because animals given water are more excitable with consequent increase of metabolism than animals deprived of water, the latter conserve their energy to a greater degree by their phlegmatic attitude. After an animal has been deprived of water for 2 weeks, there is marked irregularity in respiration; the rate may increase (double) with no increase in activity. The slower rate often is characterized by several quick breaths followed by a long pause of 2–4 s and is typical when the animal is awake; when asleep the rate is above 60 breaths/min (Howell and Gersh, 1935).

Basal metabolism is 1.2 cc  $O_2 g^{-1} h^{-1}$  (Dawson, 1955). There is an absence of a plateau in volume of oxygen consumption for *D. panamintinus* at intermediate hopping speeds (Thompson, 1985). Oxygen consumption increases markedly with decreasing ambient temperature (Dawson, 1955; Scelza and Knoll, 1975). Cold exposure initiates a significant increase in both oxygen consumption and body mass. Although both of these mechanisms are of importance, the increase in heat production is probably of greater significance than the increase in body mass to animals in the wild (Scelza and Knoll, 1980).

The zone of thermal neutrality is from 33–34°C. Above 34°C, *D. panamintinus* often will lie with limbs extended and appear lethargic. Mean body temperature at room temperature (23°C) is 36.9°C (range, 36.2–37.3). Ambient temperatures as high as 35°C can be tolerated for 12 h. Maintenance of homeothermy is facilitated by the shelter afforded by their burrows. These kangaroo rats possess limited powers of temperature regulation, despite their living in an environment characterized by wide extremes of temperature. Some individuals are unable to maintain body temperature at normal levels when exposed without food for 12 h to cool (9–16°C) ambient temperatures (Dawson, 1955). Rectal body temperature is approximately 37°C (Scelza and Knoll, 1980).

Three of seven blood composition values for *D. panamintinus* differ among seasons: red blood cell count differs between summer (mean =  $9.2 \times 10^6$ ) and autumn ( $7.9 \times 10^6$ ) and summer and winter ( $7.2 \times 10^6$ ); white blood cell count differs between spring ( $8.9 \times 10^6$ ) and the remaining seasons (range of means =  $4.6 \times 10^6$ – $6.2 \times 10^6$ ); and mean cell hemoglobin (the weight of hemoglobin in each cell) differs between summer (18.6 pg) and the remaining seasons (range of means = 20–25 pg). Range of means for the four other blood values are: hematocrit, 48.3–51%; hemoglobin, 16–17 g percent; mean corpuscular volume (volume of each individual red blood cell), 57.3–66.0  $\mu^3$ ; and mean cell hemoglobin concentration (concentration of hemoglobin distinct from whole blood), 32.2–33.0 g percent (Scelza and Knoll, 1982).

The chorioallantoic placenta of *D. panamintinus* is of the endotheliochorial type. The barrier separating the fetal and maternal bloodstreams consists of the fetal endothelium and its associated basal lamina, a single layer of trophoblast that is cellular rather than syncytial, and the maternal endothelium and its associated basal lamina (King and Tibbitts, 1969). Cells in the trophospongial layer of the placenta are involved in the accumulation and storage of glycogen and lipid and may be synthetically active (Tibbitts and King, 1975). Following parturition, the female ingests the placenta (Eisenberg and Isaac, 1963).

**ONTOGENY AND REPRODUCTION.** *Dipodomys panamintinus* routinely builds nests (Eisenberg, 1963) and has been bred in captivity (Eisenberg and Isaac, 1963). In the wild, the height of the breeding season is February or March (Harvey, 1972). However, each of four females trapped on 26 and 27 April contained

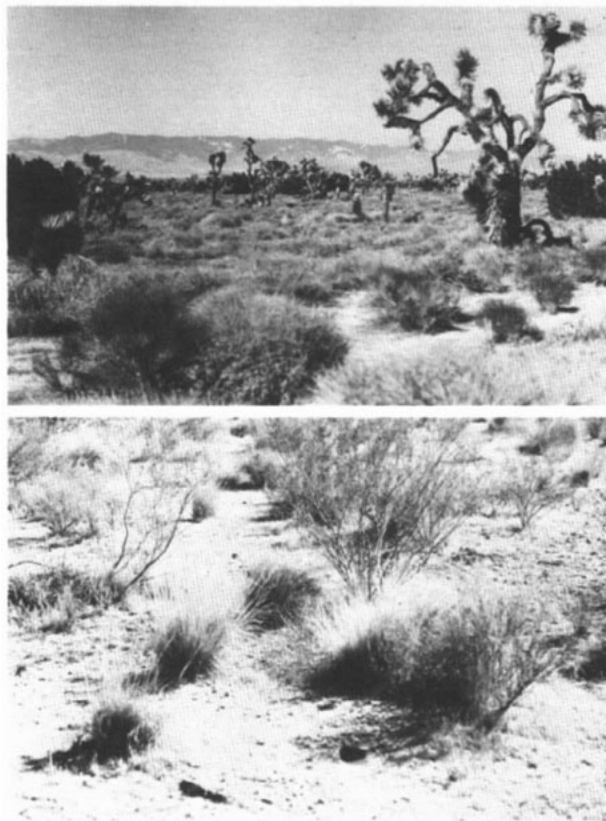


FIG. 4. Habitat occupied by *Dipodomys panamintinus* (above) and burrow entrance (below) near Pearblossom, Los Angeles Co., California. Photographs by T. L. Best.

four embryos and one taken 21 May had five embryos (Johnson et al., 1948). None taken 31 July in southern Nevada contained embryos (Hall, 1946). The gestation period is 29–30 days, litter size is 3–4 (Eisenberg and Isaac, 1963), neonate mass is 4.5 g, and total litter mass at birth, the product of neonate mass and litter size, is 15.8 g (Jones, 1985).

Eyes open at 17–18 days, auditory meatus opens at 12–14 days, dorsal pelage is completed at 10 days, and ventral pelage is completed at 14 days of age. The toes tend to be separate at birth; the cheek pouches, if represented at all, are only 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). Active grooming among siblings begins at 24 days of age, the weaning period begins at 27–29 days, the young leave the burrow at 28 days, and sexual activity begins at about 24–56 days (Eisenberg, 1963).

Young in juvenile pelage look like adults, but are decidedly paler because of less dark markings than adults. The color tone of the upper surface is nearly light buff, and the basal portion of the pelage down the mid-dorsum is dull gray. Juveniles up to the time of the post-juvenile molt can be distinguished from adults by the shortness of the hair at the end of the tail (Grinnell, 1922). One young animal taken 5 June retained some silky juvenile pelage and was on the verge of losing deciduous premolars above and below (Johnson et al., 1948).

**ECOLOGY.** In California, *D. panamintinus* occurs in areas where Joshua trees (*Yucca brevifolia*), juniper trees (*Juniperus californica*), and creosotebush (*Larrea tridentata*) are common and widely scattered (Fig. 4). Other plants may include *Ephedra viridis*, *Eriogonum wrightii*, *Tetradymia spinosa*, *Haplopappus cooperi*, *Amsinckia tessellata*, a number of grass species (Harvey, 1972), *Sarcobatus vermiculatus*, *Chrysothamnus* (Harris, 1984), *Coleogyne*, *Artemisia* (Elliot, 1904), *Eurotia lanata*, *Yucca whipplei*, *Eriogonum fasciculatum*, *Tetradymia axillaris*, *Salazaria mexicana*, *Grayia spinosa*, *Atriplex lentiformis*, and *A. parryi* (Csuti,

1969). In California, it appears that the presence of pinyon-juniper (*Pinus-Juniperus*) woodland habitat along the Santa Clara River Valley has allowed the penetration of *D. panamintinus* westward into the San Gabriel Mountains from the Antelope Valley (Csuti, 1971).

In Nevada, *D. panamintinus* is the only species of kangaroo rat that occurs in the wider, open places among pinyon trees. In southern Nevada, it occurs among *Yucca brevifolia*, *Y. mohavensis*, *Y. baccata*, and *Opuntia*, with *Acacia* in the washes (Hall, 1946). The local range of *D. p. caudatus* corresponds closely with the distribution of yuccas, covering the upper slopes of alluvial fans and penetrating at favorable places to flats in the mountains. Where an artificial clearing among the yuccas had been abandoned for several years resulting in a sparse growth of grass, *Erodium*, and weeds, these kangaroo rats are more abundant than in the surrounding undisturbed areas (Johnson et al., 1948).

In the Mojave Desert, *D. panamintinus* occurs in areas with the following average annual temperature (in °C) and relative humidity (in percent), respectively: average maximum, 25, 65; average minimum, 7, 39; and average annual, 16, 53 (Nichter, 1957). The soil may be coarse sand (Hall, 1946), gravelly desert flats (Ingles, 1965), alkaline, or the surface may be impregnated with salts and have a crust (Csuti, 1969). They avoid the vicinity of cliffs and areas with desert pavement (Johnson et al., 1948).

Panamint kangaroo rats occupy holes in small mounds of sand that have accumulated around clumps of brush (Csuti, 1969). In the Panamint Mountains, one animal may occupy a burrow that has 12 or more tunnels, the mouths of which are connected on the surface by well-defined runways (Elliot, 1904).

There is great variability in size of home range throughout the year; the average is 0.43 ha. Peaks in size of home range are in February (1.2 ha) and July (1.0 ha). Monthly fluctuations are similar to those of *D. merriami*, but the peaks are asynchronous. Home ranges tend to be elliptical in shape, especially for males in the spring (O'Farrell, 1978). There is no difference in size of home ranges between sexes. However, in the Tehachapi Mountains of California, females occupy home ranges that have significantly fewer pinyon pines (*Pinus monophylla*) than those occupied by males (Scheibe, 1984).

*Dipodomys p. leucogenys* occurs at elevations of 1,185–2,670 m, often higher than either *D. ordii* or *D. microps* (Hall, 1946). Compared to *D. merriami* and *D. deserti*, *D. p. caudatus* shows a decided preference for higher altitudes (1,140–1,620 m) and coarser soils (Johnson et al., 1948). In the Panamint Mountains, California, *D. panamintinus* occurs at elevations of 1,200–1,950 m (Elliot, 1904).

On a 2.7-ha study area in west-central Nevada, *D. ordii* was restricted to sanddune habitat and *D. panamintinus* was confined to big sage (*Artemisia*) habitat. The vegetative differences between the two habitats suggest differences in feeding strategies as well as vegetative cover (O'Farrell, 1980).

In the San Gabriel Mountains, California, cheek pouches of specimens taken early in winter contained green shoots of grass and little dry material. Frequently, *D. panamintinus* were captured at woodrat (*Neotoma*) nests beneath large junipers; many of these animals had their cheek pouches crammed full of juniper "berries" (Vaughan, 1954). Other mammals associated with *D. panamintinus* include *Perognathus longimembris*, *P. parvus*, *Chaetodipus formosus*, *Microdipodops megacephalus*, *Dipodomys microps*, *D. ordii*, *D. merriami*, *Peromyscus maniculatus* (Brown and Kurzius, 1987), *Onychomys*, *Reithrodontomys* (O'Farrell, 1974), *Ammospermophilus leucurus*, and *Neotoma lepida* (Csuti, 1969).

The coccidian *Eimeria mohavensis* was described from *D. p. mohavensis* (Doran and Jahn, 1952). *E. scholtysecki* is also found in *D. panamintinus* (Stout and Duszynski, 1983). No coccidians were found in 11 specimens from Inyo County, California (Hill and Best, 1985). Of four subspecies examined, only 8.7% of 251 *D. p. mohavensis* were naturally infected with *E. mohavensis*, which parasitizes the lower small intestine and all of the caecum (Doran, 1953).

Helminth parasites include *Gongylonema dipodomys* (Kruidenier and Peebles, 1958), *G. neoplasticum*, *Mastophorus dipodomis*, *Trypanoxyuris deserti*, *Rictularia dipodomis*, and *Catenotaenia*. The incidence of helminths in *D. p. mohavensis* ranges from 15 to 38% (Reed and Millemann, 1953). Other cestodes include *Catenotaenia californica* and *C. linsdalei* (Voge, 1955). *D. p. mohavensis* may be experimentally infected with the cestode *Oochoristica deserti* that occurs naturally in *D. merriami* (Millemann, 1955).

Fleas associated with *D. panamintinus* are *Oropsylla aridis* (Traub et al., 1983), *Meringis parkeri* (Jellison and Senger, 1976), and *Rhadinopsylla sectilis* (Holland, 1985); it probably also carries *M. dipodomys* and *Thrassis hoffmani* (Hubbard, 1961). Chiggers include *Hyponeocula arenicola*, *H. fovea*, and *H. imitator*; the characteristic sites of attachment are in a swollen pit or pustule on the ventral surface or in the cheek pouch (Tanigoshi and Loomis, 1974). The only tick reported is *Dermacentor parumapertus* (Bishop and Trembley, 1945).

**BEHAVIOR.** The Panamint kangaroo rat is a nocturnal granivore that lives on metabolic water and does not hibernate (Eisenberg, 1967). It is active throughout the year, except when there is more than 40% snow cover (O'Farrell, 1974). However, tracks of this species have been noted in the snow in the San Gabriel Mountains, California (Vaughan, 1954). Minimum temperatures (in °C) when this species is active during each season are: winter, -3; spring, -5; summer, 1; autumn, -1. There are marked sexual differences in activity for most seasons. The major tendency throughout the year is a bimodal pattern with peaks at 2 and 6–9 h after sunset; activity is low or absent towards sunrise (O'Farrell, 1974).

The species is solitary and separate except during estrus (Eisenberg, 1967). Responses between males and females change cyclically as the female passes through estrus (Eisenberg, 1963). During male–female encounters, males exhibit more sandbathing, digging, and kicking back on the days preceding or following estrus than on the actual day of estrus. The digging and kick-back patterns exhibit all the characteristics of classical displacement activity and often follow a bout of preliminary sexual behavior or chasing (Eisenberg, 1967).

Copulation involves two to three mounts lasting 30–513 s. Intervals between mounts last 1–20 s and the total duration of mounts and intervals is 8–8.5 min. This long copulatory period may have developed if copulation occurs underground in burrows (Eisenberg, 1967).

The continuous proximity of the male may cause the female to stop cycling and enter into a prolonged anestrus. Successful breeding demands that the sexes dwell separately, coming together for mating with only a brief pairing interval. The male uses a neck grip on the female while copulating (Eisenberg and Isaac, 1963).

Nonvocal auditory communication includes tooth-chattering and foot-drumming. A female uttered a repeated low-intensity, high-pitched squeal of around 2 s in length, usually when she was digging adjacent to a partition between her and a male in the next cage (Eisenberg, 1963). Vocalizations in the form of low-pitched growls also are produced by *D. panamintinus* (Blaustein and Risser, 1976).

Locomotion, though highly specialized, falls into a few major patterns. When undisturbed, the slowly moving animal travels by quadrupedal hopping, bipedal hopping, or bipedal walking. When moving rapidly, the unfrightened animal uses bipedal hopping. When frightened, the hopping becomes modified into a series of erratic bipedal leaps. The total length of the hop is approximately the length of the body. Typically, both feet are used for support anteriorly, but occasionally only one forefoot is used. The sudden and unpredictable alterations in direction of movement employed by *D. panamintinus* when attempting to escape are due not to loss of balance and control, but to the remarkably developed ability to maintain equilibrium at all times. *D. panamintinus* rarely climbs (Bartholomew and Caswell, 1951).

Fights occur when two or more animals are closely confined. Although the results of aggressive behavior are often fatal, fighting is not continuous, but consists of brief, vigorous skirmishes interrupted by periods of withdrawal (Bartholomew and Caswell, 1951).

Studies regarding the effect of water on activity are contradictory. Howell and Gersh (1935) noted that *D. panamintinus* are particularly docile in captivity, yet when given water in their diet they were more excitable. Conversely, Nichter (1957) found that at moderate humidity (59%), *D. panamintinus* fed a dry diet were hyperactive. With the addition of drinking water, activity decreased with increasing amounts of water taken. This decrease in activity was similarly maintained at low humidity (10%) on dry diet.

Where *D. merriami*, *D. ordii*, and *D. panamintinus* occur sympatrically, interspecific aggression may be one mechanism keeping them ecologically separate. In a laboratory study, *D. panamintinus* was dominant in interspecific encounters, followed by *D. ordii*, then *D. merriami* (Blaustein and Risser, 1976). *D. panamintinus* is by far more belligerent than *D. merriami*. Because *D. merriami* and *D. panamintinus* often are found in the same habitat, the

subordinate position of *D. merriami* keeps it from competing on an individual-to-individual basis with *D. panamintinus* for food and burrowing sites. In addition, the intraspecific aggressiveness of Panamint kangaroo rats may result in spacing members of this species widely enough so that the entire habitat is not fully exploited, thus leaving both space and food for *D. merriami* (Bartholomew and Caswell, 1951).

The Panamint kangaroo rat is less adept than *Perognathus* at distinguishing between food and similar non-food items. Each food item encountered is handled with the forepaws. All handling of objects is done beneath the head, well out of view of the dorsally-positioned eyes. Olfactory cues do not appear to be of major importance in distinguishing between objects. No objects, including those located directly beneath the nose, are rejected prior to being touched or manipulated. Seeds are hulled prior to pouching, resulting in a 40% more efficient use of the pouch volume (Lawhon and Hafner, 1981). Up to about nine seeds may be pouching in 1 s, with 0.09 s required for each cycle of forelimb extension and retraction during seed harvest (Price and Heinz, 1984).

Panamint kangaroo rats are excellent swimmers. Their large hind feet give them considerable agility in the water (Stock, 1972).

**GENETICS.** The fundamental number of chromosome arms is 96. There are 4 metacentric chromosomes, 9 submetacentrics, 4 subtelocentrics, 14 acrocentrics and telocentrics, the X chromosome is submetacentric, and the Y chromosome is acrocentric (Stock, 1974). The diploid number of chromosomes is 64 in all subspecies. However, the karyotype of *D. p. caudatus* differs from the other subspecies (Dingman et al., 1971); one pair of subtelocentrics in *D. p. caudatus* is very small (Stock, 1974). The lack of variation among four of the five subspecies may argue for rather recent contact among those subspecies that now appear isolated (Dingman et al., 1971).

The karyotype of *D. agilis* consists of almost all bi-armed pairs. Because the karyotype of *D. panamintinus* contains one-half unpaired pairs, it may be used to distinguish between these species (Csuti, 1969). For a laboratory culture of cells from *D. panamintinus*, there was no obvious relationship between C, G, or Q-banding regions of chromosomes and a particular S-phase time of replication of the DNA in these banded regions (Bostock and Christie, 1975).

The nuclear DNA content for *D. panamintinus* is 7.9 pg (Hatch et al., 1976). The percent of the total area under an analytical ultracentrifuge scan of ultraviolet absorbance in neutral CsCl density gradients indicates the following proportions of DNA components in *D. panamintinus*: principal, 44; intermediate, 26; and two satellite DNA components totaling 30% (Mazrimas and Hatch, 1972). Conditions for optimal separation of DNA in density gradients for *D. panamintinus* are: initial density, 1.525 g/ml; M ratio of Ag<sup>+</sup>/DNA-P, 0.29;  $\mu\text{g AgNO}_3/\mu\text{g DNA}$ , 0.154. The strand densities for a given satellite DNA are nearly identical among species of *Dipodomys* (Mazrimas and Hatch, 1977).

Genic analysis revealed the mean number of alleles per locus for two populations was 1.0, the mean proportion of loci polymorphic per population was 0.0, and the mean proportion of loci heterozygous per individual was 0.0. None of 11 other species of *Dipodomys* examined exhibited so little genic variation. *D. panamintinus* has a hemoglobin indistinguishable from *D. heermanni* and *D. agilis*, and the lactate dehydrogenase-5 allozyme is shared with *D. panamintinus*, *D. elator*, *D. merriami*, *D. microps*, and *D. spectabilis*. *D. panamintinus* from near Hesperia, California, is monomorphic for a transferrin-1 allele that is not represented in the population near Carson City, Nevada, but occurs in high frequency in *D. agilis*. Both *D. panamintinus* and *D. microps* have low levels of heterozygosity, unlike other members of the *heermanni* species group (Johnson and Selander, 1971).

**REMARKS.** *Dipodomys* is from the Greek words *di* (two), *podos* (foot), and *myos* (mouse; Jaeger, 1955) that refer to its enlarged hind feet and bipedal mode of locomotion. The name *panamintinus* refers to the Panamint Mountains, California, where the type specimen was collected.

*Dipodomys panamintinus* apparently represents an earlier derived population that may have been isolated from populations leading to *D. heermanni* by the rise of the Tehachapi Range and perhaps also by changing climatic conditions. The wane of Wisconsin Pluvial conditions left "islands" of *D. panamintinus* above the desert floor; a small amount of karyotypic difference already exists between some of these populations reflecting their isolation (Stock, 1974).

Attempts have been made to arrange kangaroo rat species into groups that are intended to show phylogenetic relationships. Grinnell (1921) placed *D. panamintinus* in the *heermanni* group with *D. californicus*, *D. heermanni*, *D. ingens*, and *D. stephensi*. Subsequent studies to elucidate relationships between *D. panamintinus* and other species of *Dipodomys* have examined: skeletal and visceral measurements (closest affinities are with *D. stephensi*; Setzer, 1949); field experience (*D. gravipes*, *D. heermanni*, *D. ingens*, and *D. stephensi*; Lidicker, 1960a); structure of the molariform teeth (*D. spectabilis*, *D. microps*, *D. nelsoni*, and *D. agilis*; Nader, 1966); protein variation (*D. agilis* and *D. heermanni*; Johnson and Selander, 1971); percent of satellite DNA compared to indices derived from lengths of limb bones (*D. agilis*; Mazrimas and Hatch, 1972); percent of satellite plus intermediate DNA and the fundamental number of chromosome arms (*D. ingens*, *D. heermanni*, and *D. merriami*; Mazrimas and Hatch, 1972); bacula (*D. deserti*, *D. merriami*, and *D. phillipsii*; Best and Schnell, 1974); chromosomes (*D. ingens* and *D. heermanni*; Stock, 1974); immunologic distance (*D. agilis*, *D. californicus*, and *D. heermanni*; Hatch and Mazrimas, 1977); phenetic analyses of skeletal characters (an outlier, but its closest affinity is with the *heermanni* group; Schnell et al., 1978); and phenetic analyses of cranial characters (*D. heermanni* and *D. stephensi*; Best, in press).

H. T. Haagenstad prepared Fig. 3. T. E. Garrison assisted in gathering the literature. F. S. Dobson, M. J. O'Farrell, G. Hepp, R. S. Lishak, S. B. George, and D. F. Williams critically evaluated an early draft of the manuscript. This is journal article no. 15.892069P of the Alabama Agricultural Experiment Station.

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