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Peromyscus crinitus.

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Canyon Mouse

Hesperomys crinitus Merriam, 1891:53. Type locality, Shoshone Falls, N side Snake River, Jerome Co., Idaho.
Sitomys auripectus J. A. Allen, 1893:75. Type locality, Bluff City, San Juan Co., Utah.
Peromyscus stephensi Mearns, 1897:721. Type locality, 3 mi. E Mountain Spring, Imperial Co., California.
Peromyscus petraius Elliot, 1904:244. Type locality, Lone Pine, Inyo Co., California.
Peromyscus crinitus, Bangs, 1899:67. First use of name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Sigmodontinae, Genus *Peromyscus*, Subgenus *Peromyscus*; *crinitus* species group. The genus *Peromyscus* includes 49 nominal species (Honacki et al., 1982), several of which are insular forms. The species group includes *Peromyscus pseudocrinitus* Burt, a species endemic to Coronados Island, Gulf of California, and *Peromyscus caniceps* Burt, endemic to Monserrate Island, Gulf of California.

Subspecies were reviewed by Hall and Hoffmeister (1942). Hall (1981) listed eight subspecies, as follows, and mapped their geographic ranges:

P. c. auripectus (J. A. Allen, 1893:75), see above.
P. c. crinitus (Merriam, 1891:53), see above (*peridoneus* Merriam a synonym).
P. c. delgadilli Benson, 1940:1. Type locality, 2 mi. S Crater Elegante, 34 mi W Sonoita, Sierra del Pinacate, Sonora.
P. c. disparilis Goldman, 1932:90. Type locality, Tinajas Altas, 2,000 ft, Gila Mts., Yuma Co., Arizona (*rupicolus* Benson and *scopulorum* Benson are synonyms).
P. c. doutti Goin, 1944:189. Type locality, Antelope Canyon, 7,200 ft, 20 mi SE Duchesne, Duchesne Co., Utah.
P. c. pallidissimus Huey, 1931:389. Type locality, small island in Gonzaga Bay, 29°50′N, 114°20′W, Baja California.
P. c. pergracilis Goldman, 1939:356. Type locality, S end Stansbury Island, 4,250 ft, Great Salt Lake, Tooele Co., Utah.
P. c. stephensi Mearns, 1897:721, see above (*petraius* Elliot a synonym).

DIAGNOSIS. Accessory cusps between three principal labial cusps of M1 and m1 rudimentary or lacking; palate nearly as long as incisive foramina; dorsal pelage long, lax, silky; tail as long as or longer than head and body; two pairs of mammae, inguinal.

GENERAL CHARACTERS. The following description of *Peromyscus crinitus* (Fig. 1) was compiled from Benson (1940), Davis (1939), Hall (1946), Hall and Hoffmeister (1942) and Osgood (1909) and confirmed by re-examination of specimens in the University of Colorado Museum. Capitalized color terms are from Ridgway (1912) as reported by Benson (1940) and Hall and Hoffmeister (1942).

Size small to medium for genus; tail generally longer than head and body except in some northern populations; ears large, about same length as hind foot, sparsely haired. Means, extremes (in parentheses) and sample sizes for external measurements (in mm) of adult males and adult females, respectively, from throughout the range of the species in the United States are: total length, 174.6 (162 to 186), 79, 176.1 (164 to 191), 81; length of tail, 91.6 (82 to 101), 79, 92.2 (79 to 118), 81; length of hind foot, 20.7 (18 to 25), 79, 20.6 (18 to 22), 81; ear, 19.9 (17 to 23), 69, 20.1 (18 to 22), 79; mass (in g), 16.52 (12.8 to 20.5), 52, 17.3 (12.6 to 22.9), 49 (Armstrong, 1972, 1982; Davis, 1939; Durrant, 1952; Hall, 1946; Hall and Hoffmeister, 1942). Benson (1940) provided measurements of Mexican specimens, but included subadults in means; hence, the data are not readily comparable with those reported herein.

Geographic variation in size generally is clinal (Hall and Hoffmeister, 1942). Animals from the north have longer and heavier bodies, relatively and absolutely shorter tails, and larger skulls. In addition to geographic variation, there appears to be sexual dimorphism, with females averaging larger than males. Hall (1946) reported females to be 3.5% longer, 17.5% heavier, and to have 2.1% longer skulls.

Tail thinly covered with long, soft hairs, sometimes appearing distichous or crested; annulations of epidermal scales generally readily visible beneath hairs of tail; distinctly penicillate; usually distinctly bicolored, countershaded (dark above, pale below). Feet white (except black in *P. c. delgadilli*), haired only on proximal fourth of plantar surface; dorsal pelage long and lax, silky, often appearing ruffled; individual hairs lead-gray at base, succeeded by ochraceous to buffy subterminal band, and tipped with brown or black; dark grayish bases of hairs sometimes visible through buffy to pale grayish shade of dorsum; color usually becomes less bright (and more grayish) with age; hairs of forehead, nose, and face shorter than those of body; color of those areas appearing slightly more grayish than body as bases of hairs more readily visible.

Dorsal color geographically variable. Hair Brown overlain with ochraceous in *P. c. crinitus*—northern Nevada, Oregon, Idaho; Light Ochraceous-Buff, lightly overlain with dusky in *P. c. pergracilis*—Bonneville Basin; Light Ochraceous-Buff overlain with brownish or blackish in *P. c. stephensi* and *P. c. disparilis*—lower Colorado drainage and southern California; Pale Ochraceous-Buff overlain with brownish and dusky in *P. c. pallidissimus*—an insular form in the Sea of Cortez; Chaetura Drab in *P. c. delgadilli*—Pinacate Lava Flow, Sonora; Ochraceous-Buff in *P. c. auripectus*—Colorado Plateau (Hall and Hoffmeister, 1942); Light Ochraceous-Buff to Light Pinkish Cinnamon in *P. c. doutii*—Uinta Basin (Goin, 1944). Individuals darker dorsally tend to have clear buffy lateral line. Venter white (except in *P. c. delgadilli*), hairs gray at base; buffy to ochraceous pectoral patch (especially pronounced in *P. c. auripectus*, perhaps least so in *P. c. doutii*); venter sometimes faintly washed with buff; ochraceous anal patch sometimes present.

As in some other rodents, canyon mice sometimes have the general color of their characteristic substrate, thereby forming microgeographic color races. An early critical review of this phenomenon (Sumner and Swarth, 1924) had too few specimens of canyon mice to permit conclusions. Benson (1940) described three dark-colored subspecies from Sonora, based on populations from localities with dark substrates. Hall and Hoffmeister (1942) relegated two of those nominal subspecies (*P. c. rupicolus* and *P. c. scopulorum*) to synonymy under *P. c. disparilis*, but retained the third (*P. c.*

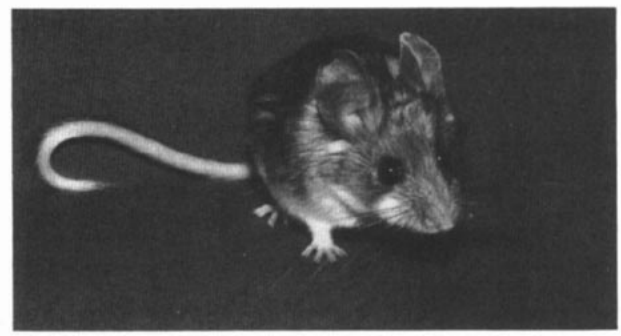

FIG. 1. Photograph of captive *Peromyscus crinitus* from San Juan Co., Utah. Photograph by senior author.

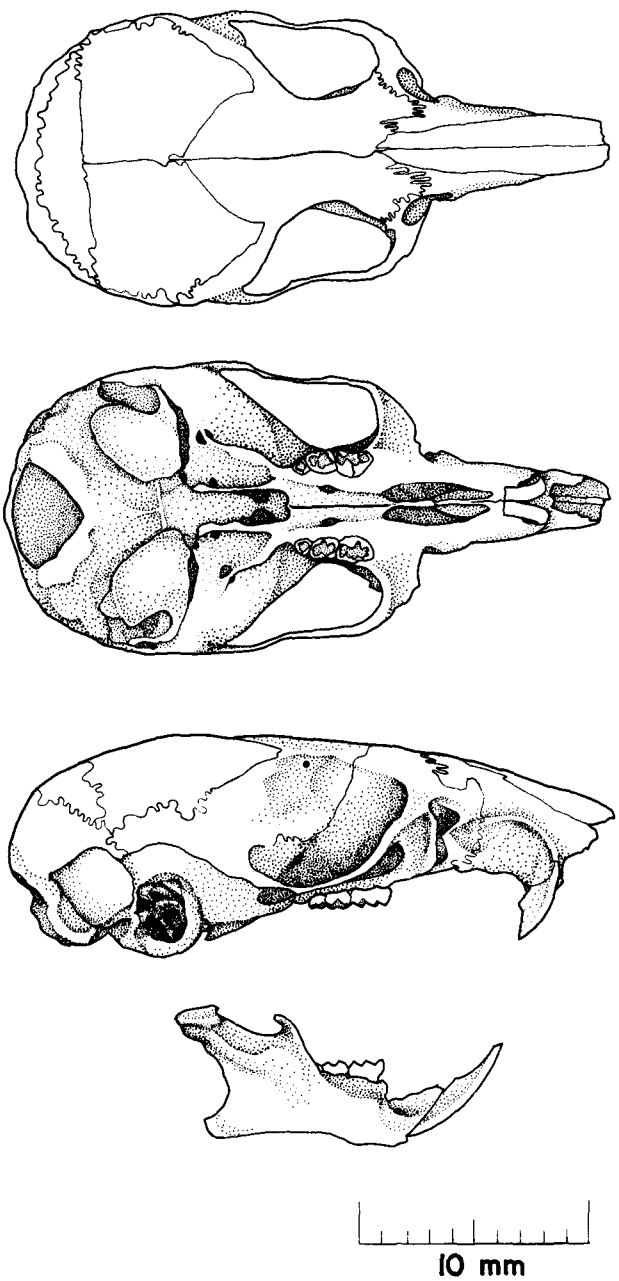

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Peromyscus crinitus* (University of Colorado Museum No. 15374, adult female) from San Juan Co., Utah. Drawing by Genevieve Lee.

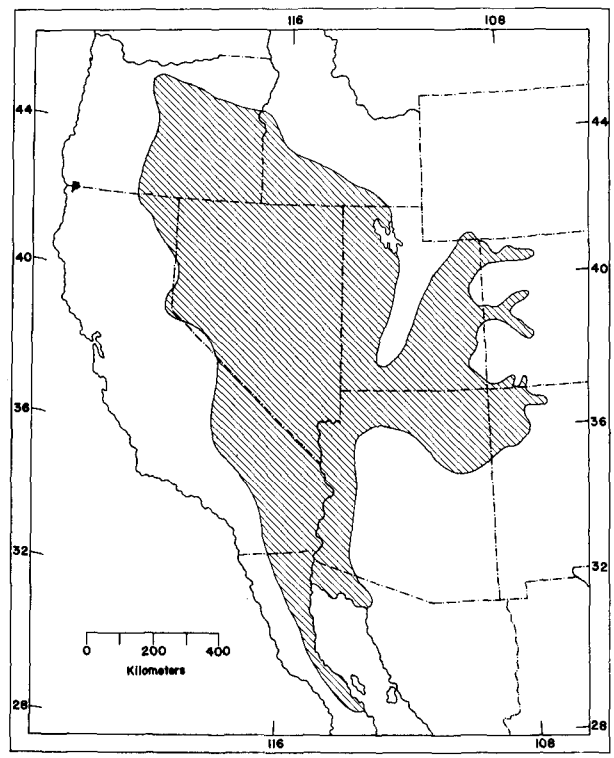

FIG. 3. Map showing geographical distribution of *Peromyscus crinitus*.

delgadilli) as a valid subspecies. Hardy (1941) commented on the dark color of canyon mice from St. George, Utah, and later, he noted that canyon mice in southwestern Utah vary in color according to the predominant color of rocky substrates (Hardy, 1945). Although microgeographic "tracking" of substrate color appears to be common, it is not an inviolate rule; canyon mice from areas of pale granite and black lava in Arizona were generally uniform in color (Dice and Blossom, 1937).

Skull (Fig. 2) rather delicate; braincase broad, shallow, flattened, rounded in dorsal view; rostrum relatively long and slender, slightly depressed, more or less rounded dorsally; nasals long, slender, somewhat compressed posteriorly; infraorbital canal high, relatively narrow; zygomata rather delicate, zygomatic breadth not much greater than cranial breadth; ascending branches of premaxillae usually attenuate and rarely extending behind nasals; auditory bullae of moderate size; maxillary toothrow short; palate nearly as long as incisive foramina; means, extremes (in parentheses) and sample sizes for cranial measurements (in mm) of adult males and adult females, respectively, from throughout the range of the species in the United States, are: greatest length of skull, 24.9 (23.8 to 26.3), 88, 25.0 (23.0 to 26.2), 78; condylobasal length, 24.0 (22.8 to 24.8), 34: 23.8 (22.9 to 24.8), 31; zygomatic breadth, 12.5 (11.5 to 13.0), 46; 12.4 (11.6 to 12.7), 37; interorbital constriction, 4.4 (3.8 to 4.9), 88, 4.3 (3.8 to 4.8), 84; length of nasals, 9.5 (8.4 to 10.6, 88, 9.5 (8.6 to 10.1), 78; length of maxillary toothrow, 3.5 (3.2 to 3.9), 88, 3.6 (3.2 to 3.8), 78; cranial depth, 8.8 (8.6 to 9.3), 34, 8.8 (8.6 to 9.0), 31 (Armstrong, 1972, 1982; Durrant, 1952; Hall, 1946; Hall and Hoffmeister, 1942).

Dental pattern simple, much like *P. eremicus*; accessory lophs typically absent; presence of accessory styles geographically variable; when present, unattached to neighboring cusps or lophs; no mesoloph; lower teeth simpler than upper teeth, no meso- or ectolophids, and stylids small and present in one-third of sample; details and frequency distributions of dental traits provided by Hooper (1957). Armstrong (1979*a*), Hall (1946), Hall and Hoffmeister (1942), and Kelson (1951) provided additional comments on phenotypic variation.

DISTRIBUTION. The canyon mouse occurs in western United States and adjacent northwestern México, from Oregon, Idaho, and Wyoming southward to Sonora and Baja California Norte, and from California east to Colorado and New Mexico (Fig. 3).

Physiographically, the range encompasses much of the Intermontane Plateaus Division that includes the southern Columbia Plateau, Basin and Range, and Colorado Plateau provinces, an area west of the Rocky Mountains and east of the Sierra Nevada (except in southern California, where canyon mice occur in the Kern River drainage). Reported elevational range is from 85 m below sea level in Death Valley to 3,230 m at Bullfrog Lake, Fresno Co., California (Hall and Hoffmeister, 1942).

The canyon mouse is restricted to the Navahonian, Artemisian, Mohavian, and Sonoran Biotic Provinces of Dice (1943). These correspond roughly to the Navahonian, Uintian, Artemesian [sic], Mohavian, Kaibabian, and Sonoran "mammal provinces" of Hagmeier (1966). Areographically, Armstrong (1972, 1977) included the species in the Yuman Faunal Element.

Figure 3 is based on Hall (1981), who listed marginal records. Within the range mapped, *P. crinitus* often is restricted to canyons that extend in a dendritic pattern into areas of otherwise unsuitable

habitat. Furthermore, within the range outlined, canyon mice often are absent from habitat that seemingly is suitable for them. Hence, the actual range of *P. crinitus*, both regionally and locally, is considerably smaller than an uncritical glance at the range map suggests. Details of local distribution within the range mapped were provided by Armstrong (1972, 1982), Bailey (1936), Cockrum (1960), Davis (1939), Durrant (1952), Findley et al. (1975), Goldman (1937), Hall (1946), Kirkland (1980), and Long (1965).

Subspecies are not reviewed in this paper and subspecific boundaries are not indicated in Fig. 3. The interested reader is referred to the review by Hall and Hoffmeister (1942) or the compilation by Hall (1981).

FOSSIL RECORD. The earliest fossils of *P. crinitus* are from Rancholabrean deposits (100,000–130,000 YBP) from the Newport site in the Los Angeles Basin (Miller, 1971). An association with *Dipodomys* and *Perognathus californicus* suggests a semiarid climate for this coastal site. The canyon mouse no longer occurs there. Harris (1970) tentatively identified *P. crinitus* as a member of the Dry Cave Fauna (14,470 ± 250 YBP) in southeastern New Mexico, approximately 450 km SE of the present range. A drier climate in the 13th Century apparently allowed the canyon mouse to occur to the east and southeast of its present range (Holbrook, 1977, 1980).

FORM. Few aspects of the anatomy of the canyon mouse have been studied, and we are largely ignorant of morphological adaptations of *P. crinitus* to their characteristically demanding habitat. Klingener (1968) made only incidental reference to *P. crinitus*, but the interested reader is referred to that summary for general description of the morphology of species of *Peromyscus*. Hooper (1957) described dental patterns in canyon mice.

The distal tract of the glans penis is short, about two-fifths the length of the hind foot. The glans is rod-shaped, flared distally. Its length is about four times its greatest diameter and about one-fourth the length of the hind foot. The surface is covered with spines, slightly larger and more distantly spaced proximally than distally. There are two dorsal lappets and a ventral lappet arranged about the urethral orifice. A cone of nonspinous, soft tissue distal to the urethral opening is slightly protractile (Hooper, 1958).

Mean and extreme (in parentheses) measurements (in mm) of four bacula (Burt, 1960) were: length, 8.2 (7.5 to 8.6); width of base, 1.8 (1.5 to 2.1). The structure is curved dorsoventrally near the tip (Blair, 1942; Burt, 1960), concave above and below, and slightly expanded at the tip, capped with a minute cartilaginous cone (Hooper, 1958). The baculum is similar to that of *P. eremicus* (Blair, 1942; Burt, 1960). It is relatively shorter (one-third the length of the hind foot) than in any other member of the "*Maniculatus* division," more similar to *P. gossypinus* and *P. polionotus* than to *P. truei* or *P. boylei* (Hooper, 1958).

Mean measurements (in mm) of reproductive tracts of three males from Kern Co., California, were: testis, 7.0 by 4.0; ductus deferens, 10.4; urethra, 8.5; ampullary gland, 1.9 by 2.5; vesicular gland, 5.1 by 2.3; anterior prostate gland, 3.2 by 1.2; dorsal prostate, 3.7 by 1.9; ventral prostate, 2.2 by 1.3; bulbourethral gland, 1.8 by 1.8. Preputial glands are absent, the urethra relatively short, and the ventral prostate relatively small; otherwise, *P. crinitus* is typical of the subgenus *Peromyscus*, lying intermediate between *maniculatus* and *boylii* species groups. There are one pair each of ampullary, vesicular, anterior and dorsal prostates, and bulbourethral glands, and two pairs of dorsal prostates (Linzey and Layne, 1969).

FUNCTION. Under laboratory conditions, canyon mice are independent of free, exogenous water when fed dry food (Abbott, 1971; MacMillen, 1972; MacMillen and Christopher, 1974). Deprived of water, canyon mice equaled or exceeded the performance of *Dipodomys merriami* in both weight response and osmolarity of urine (MacMillen, 1983; MacMillen and Christopher, 1974). Without a source of water, *P. crinitus* lost 10% of its body weight in 7 days, then maintained body weight indefinitely (MacMillen, 1983). In the laboratory, urine concentration was 3,420 mOsm/l (Abbott, 1971). Under field conditions, canyon mice produced urine in excess of 4,000 mOsm/l and had a blood plasma osmotic pressure of 350 mOsm/l throughout the year (MacMillen, 1983; MacMillen and Christopher, 1974). Although canyon mice apparently can prevail without water, Ryan (1968) observed them to drink from a water hole in Deep Canyon, California. Fluid consumption decreased when NaCl concentrations exceeded 0.38 M, but canyon mice gained or maintained weight when consuming solutions with concentrations to 0.67 M; on a 1.0 M NaCl regimen, they lost weight but survived (Abbott, 1971).

Canyon mice exhibit diurnal torpor in response to food (Morhardt and Hudson, 1966) and water (MacMillen, 1983) deprivation. Drought-induced torpor, common in *Peromyscus* from arid environments, might enhance ability to cope with xeric habitats (MacMillen, 1983).

In comparison to other *Peromyscus* species, *P. crinitus* had a body temperature 0.9°C lower than predicted from body size (McNab, 1968; McNab and Morrison, 1963). Members of third generation laboratory colonies continued to show this trait (McNab and Morrison, 1963). *P. crinitus* had a lowered body temperature in response to cold stress or food shortage (or both) in nature and some individuals were active with lower than normal body temperatures (Mullen, 1971). At environmental temperatures between 1 and 5°C, some individuals ceased to regulate body temperature and entered torpor (McNab and Morrison, 1963).

In the field in November, January, and February, CO_2 production was 4.54, 4.40, and 7.51 $ml^{-1}\ g^{-1}\ h$ respectively, and O_2 consumption was 5.53, 5.37, and 9.15 $ml^{-1}\ g^{-1}\ h$. Average body mass increased from 12.4 g in November to 13.2 g in January, and 16.0 g in February (Mullen, 1971).

Dry-weight biomass is 4.49 ± 0.35; percentage fat, 16.97 ± 2.36; percentage ash, 13.78 ± 0.60; caloric density, 5.21 ± 0.11 kcal/g dry weight, 6.05 ± 0.10 kcal/g ash-free dry weight (Kaufman et al., 1975). Wiener et al. (1977) published details of ash composition.

Frequency of intrinsic intestinal contraction in the canyon mouse was a function of gut temperature (Studier et al., 1977). Gut thermal sensitivity in *P. crinitus* was significantly less than in *P. eremicus*, and significantly greater than in *P. leucopus*. Kenagy and Hoyt (1980) observed coprophagy in the canyon mouse.

ONTOGENY AND REPRODUCTION. The estrous cycle is typical of muroid rodents (Dewsbury et al., 1977). Ovulation is spontaneous. Mean length of the estrous cycle (n = 7 individuals, 30 cycles) was 6.1 days; mode, 5 days; median 4.9 days ($\pm SE$, 1.3).

At lower elevations (1,370 m) on White Mountain, Mono Co., California, breeding occurred mostly in spring (March and May sampling periods). At 2,165 m, breeding canyon mice were taken in spring (March and May) and fall (October), and were reproductively inactive in midsummer and midwinter (Dunmire, 1961). In a laboratory colony from Utah, young were born in every month, but 109 of 135 litters (81%) were born from January through August; fewest litters were born in November (Egoscue, 1964).

The animals are seasonally polyestrous; many females showed the same breeding period each year. Females averaged 2.05 litters per year with a maximum of eight. The maximum reproductive lifetime of a captive female was 46 months. The shortest interval between successive litters was 27 days. Gestation while lactating lasted 29 to 31 days; gestation for nonlactating females was 24 to 25 days (Egoscue, 1964).

Litter size ranged from one to five (mean, 3.1, mode, four; Egoscue, 1964). Just one of 130 litters contained five young (females have four mammae). Embryo counts from field studies (for example, Armstrong, 1982; Davis, 1939; Egoscue, 1964; Hall, 1946) all were between one and five. Male : female sex ratio was 68:75 (0.91:1) at 1,370 m and 143:148 (0.97 to 1) at 2,165 m in California (Dunmire, 1961).

In a laboratory colony bred from stock obtained from San Diego Co., California, mean litter size was 2.9 ($\pm SE$ = 0.07, n = 206), significantly smaller than in *P. leucopus*, *P. maniculatus*, or *P. polionotus* (Drickamer and Vestal, 1973). The rate of destruction of litters (26.9%) was the highest reported among 10 species compared. Mean litter size increased from 2.5 for primiparous females to three or more in successive litters. In the laboratory, there was no reproductive seasonality and no relationship between breeding activity and day length.

Neonates appeared slightly more advanced (by 2.5 to 3 days) than newborn deer mice, and weighed an average of 2.2 (1.8 to 2.6) g. The tail averaged 12.8 (12 to 14) mm long, the hind foot, 7.5 (7 to 8). Neonates were lightly pigmented above and vibrissae were present. Ears were folded against the head and the animals squeaked faintly. By 1 week of age young weighed 5 to 6 g. Short black fur and scattered guard hairs were apparent on the dorsum,

and sparse hair was visible on the venter. The vibrissae were about 10 mm long, but the tail still was hairless. Eyes opened at 15 to 17 days of age. At 4 weeks, the animals weighed 13.2 to 15.0 g and were weaned. Juveniles were uniformly pale gray, without brown overtones and with few black-tipped hairs (Egoscue, 1964).

Among 18 species of *Peromyscus* the canyon mouse was distinctive in its relatively long period of lactation (28 days in comparison with a mean for 18 species of 21.9 days) and high relative birth mass (birth mass/adult mass, 0.47 in comparison with a mean for 18 species of 0.28), traits interpreted as responses to an unproductive habitat (Modi, 1984). Age at weaning used by Modi (1984) was based on Egoscue (1964) and is the maximum reported for the species. Drickamer and Vestal (1973) reported the average age at weaning as 23 days; the range in 10 species of *Peromyscus* studied was 21 to 30 days. Eisenberg (1968) reported weaning at 24 to 26 days of age; females routinely carried young attached to the nipples. Breeding may commence as early as 70 days, but most pairs did not begin to breed until 4 to 6 months of age. Longevity has not been studied.

There are two maturational molts (postjuvenile, postsubadult) and a seasonal molt or molts. Examination of specimens in the University of Colorado Museum suggests that the postsubadult molt is patchy and irregular, with the first buffy hairs appearing on the sides, rump, or middorsum. We have specimens to document molt in adults in summer, exhibited as an anterior to posterior wave of replacement obvious in July-taken males from Colorado and Utah; molt appears to be retarded or postponed in lactating females.

In common with other xeric-adapted species (*P. eremicus*, and *P. californicus*), canyon mice have relatively precocial young. In common with *P. truei*, postnatal development is relatively slow and protracted, a pattern perhaps related to unproductive habitat (Layne, 1968). Based on a plot of adult body mass against the sum of gestation period plus days to eye-opening for several cricetines, *P. crinitus* showed slow development, especially relative to *P. eremicus* and *P. californicus* (Eisenberg, 1981). More complete data on ontogeny of many species of *Peromyscus* are required to understand these patterns.

ECOLOGY. Canyon mice occur exclusively in rocky habitats: gravelly desert pavement, talus, boulders, cliffs, and slickrock (Armstrong, 1979*a*, 1979*b*, 1982; Baker, 1968; Bradley and Mauer, 1973; Egoscue, 1964; Harris, 1963; Hayward et al., 1958; Hoffmeister and Durham, 1971; Johnson, 1981; Matson, 1976; Presnall, 1938; Ruffner et al., 1978). Vegetation has little or no effect on local distribution; the species is associated with rocky substrate rather than any particular plant association (Deacon et al., 1964; Egoscue, 1964; Johnson, 1983). Where rocky, rough, and broken terrain occur, canyon mice have been captured in association with blackbrush (*Coleogyne*; Armstrong, 1979*b*), yellow pine (*Pinus ponderosa*)-fir (*Abies*)-aspen (*Populus tremuloides*; Burt, 1934), piñon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodland (Deacon et al., 1964), *Larrea-Franseria*, *Emplectocladus*, and *Atriplex-Hilaria* communities (Hardy, 1945), *Artemisia*, *Atriplex*, *Coleogyne*, and *Larrea* (Honeycutt et al., 1981), *Grayia-Lycium*, *Atriplex-Kochia*, *Salsola*, and piñon-juniper communities (Jorgensen and Hayward, 1965), and creosote (*Larrea*)-palo verde (*Cercidium*) and *Agave-Ocotillo* communities (Ryan, 1968).

Canyon mice are omnivorous (Morton, 1979). In California and southern Nevada, they ate seeds, insects, and green vegetation in amounts depending on seasonal availability (Bradley and Mauer, 1973; MacMillen and Christopher, 1974). Insects and other small animals compose a significant proportion of the diet when seeds are rare (MacMillen, 1972). Seeds composed most of the diet in southeastern Utah (Armstrong, 1982). In captivity, canyon mice ate mealworms (*Tenebrio*; Ryan, 1968).

Canyon mice traveled as fast as 27.3 m/min (Fisher and Cross, 1979). By use of the adjusted convex-polygon method, Johnson (1976) found no statistically significant differences between sizes of home ranges ($\bar{X}$ + 1 *SE*) of seven males (0.35 + 0.029 ha) and six females (0.38 + 0.084 ha) in southeastern Utah. Densities have been reported as 0 to 26.5/ha in the Grand Canyon (Ruffner et al., 1978), 0.5 to 3.0/ha in *Agave-Ocotillo* in California (Ryan, 1968), and 0.5 to 42.9/ha in southeastern Utah (Johnson, 1981, 1983). On isolated buttes the latter author found densities ranging from 5 to 42.9/ha. When open space between shrubs was decreased with artificial shelters (thereby decreasing the risk of predation) abundance of *P. crinitus* increased (Thompson, 1982), suggesting that risk of predation influenced density. Tanner (1965) reported an apparent population crash of all small mammals (including *P. crinitus*) at a site in Utah.

Canyon mice may compete with other omnivorous/granivorous rodents. Where *Neotoma lepida* was removed, populations of *P. crinitus* and *P. eremicus* increased by 87%. Where *Perognathus fallax* was removed, *Peromyscus* populations increased 130% (Eidemiller, 1980). Where canyon mice and cactus mice are sympatric, canyon mice occupy rocky areas and cactus mice inhabit brushy flats on the desert floor (Eisenberg, 1963). However, *P. crinitus* was outnumbered by *P. eremicus* in rocky terrain in Deep Canyon, California (Ryan, 1968).

Johnson (1981, 1983, 1986) studied mammalian communities on five island-like isolated buttes and a nonisolated site in southeastern Utah. *P. crinitus* was the only terrestrial mammal found on all buttes. On one butte, the canyon mouse was one of only two mammalian species, and on another butte it was the only species of *Peromyscus*. In contrast, the nonisolated control site supported at least 16 mammalian species. Where the canyon mouse was the sole or most abundant *Peromyscus*, it used a broad range of microhabitats. Where *P. crinitus* occurred with two or three other species of *Peromyscus*, it was restricted to rocky microhabitats. In addition, the density of canyon mice was correlated inversely with mammalian species richness. Johnson (1986) speculated that interspecific competition restricted canyon mice to rocky habitats and also suggested that the canyon mouse was the only terrestrial mammal to occur on all of the isolated buttes because it is an excellent climber and xeric-adapted. The sheer cliffs that form the isolated buttes might not be a barrier to movement of canyon mice to the summit of a butte, but actually might be suitable habitat. Most other mammalian species cannot surmount the cliffs to colonize summits of buttes.

Whitaker (1968) reported two endoparasites from the canyon mouse, a cestode and a thelaziid nematode. Babero and Matthias (1967) reported a 22% infection rate of *P. crinitus* by the oxyurid nematode, *Syphacia paromysci*, in Clark Co., Nevada. Grundmann (1957) reported *Protospiura numidica* from 41% of canyon mice in the Great Salt Lake Desert.

Whitaker (1968) summarized an extensive ectoparasite fauna for the canyon mouse, including 20 species of mites, 6 chiggers, 3 ticks, and 1 louse. Since that compilation, Stark and Kinney (1969), Egoscue (1976), and Armstrong (1982) reported 10 additional fleas from the canyon mouse, and Allred and Beck (1966), Armstrong (1982), and Goff and Loomis (1973) reported three other acarines.

Botfly (*Cuterebra*) parasitism of *P. crinitus* has not been reported in the literature, and Hall (1946) explicitly commented on the absence of warbles from *P. crinitus* in Nevada. Eighteen of 257 individuals that we captured in southeastern Utah were infested; some carried two larvae simultaneously.

Allred (1956) and Whitaker (1968) compared the occurrence of mites of five species of *Peromyscus* from Utah. Differences found were attributed to habitat requirements of both mice and mites. *P. crinitus* was particularly prone to infestation by *Eubrachylaelaps hollisteri*. Egoscue (1976) reported that where *Peromyscus crinitus* and *P. maniculatus* were sympatric in western Utah, 20.8% of flea-infested canyon mice had deer mouse fleas and 18.9% of flea-infested deer mice had fleas of the canyon mouse.

Canyon mice were not infected with sylvatic plague at Lava Beds National Monument, California, where the disease occurred in *P. maniculatus* and *Neotoma cinerea* (Nelson and Smith, 1976), because canyon mice were restricted to the twilight zone of the caves, hence did not encounter dens of woodrats (*Neotoma cinerea*).

BEHAVIOR. Dewsbury (1975) described copulatory behavior. At first the female ran from the male; then she adopted a stationary receptive posture with the perineum elevated. The male mounted from behind. Average latency to first intromission was 1,314 s (range, 50 to 3,969). Several short thrusts preceded intromission. Intromissions were a single deep thrust with rapid dismount. There was no lock. Duration of intromission was about 0.25 s. Multiple intromissions preceded ejaculation. A mean of 2.2 (range, 1 to 4) ejaculations preceded satiety.

In captivity, females did not allow males in the nest box during parturition and male intruders often were bitten on the rump and tail (Eisenberg, 1963). At times other than at parturition, female-female encounters were less likely to result in fights than male-male encounters. Male-female encounters were more aggressive than female-female encounters but less so than male-male encounters. These

results indicate a dispersed social organization with high male-male antagonism and only moderate pair bonding (Eisenberg, 1963). Adult groupings probably are limited to brief pairings of females and males for copulation. After birth, females and young nest separately from males.

Peromyscus crinitus quickly learned complex mazes without extrinsic rewards, such as food and water (Brant and Kavanau, 1964, 1965; Kavanau, 1963, 1967). By day, mice left the nest briefly to eat, drink, and eliminate. At night, in dim light, they spent 83% of their active time running on a wheel, then returned to the nest 2 to 4 h before daylight. When several mice lived together, they displayed synchronous activity patterns (Kavanau, 1967). Canyon mice were avid wheel-runners and quickly learned to press a lever to release a clutch for free-wheel running (Kavanau, 1963).

Captive canyon mice were most active at light intensities from 4.5×10^{-3} to 6.0×10^{-1} lux (Kavanau and Havenhill, 1976). This range of illumination encompasses full-moon intensity (2×10^{-1} lux) and corresponds to occupation of open habitats and consequent exposure to brighter light. Wheel-running speed was directly proportional to light level from 0.6 to 3.6 lux, then decreased quickly. Canyon mice ran on wheels with hurdles or gaps that had to be jumped (Kavanau and Havenhill, 1976). In nature, the mice move as fast as navigational safety allows in prevailing light conditions (Kavanau, 1967).

Eisenberg (1968) described vocal and nonvocal auditory communication. The abandoned cry of neonates was scarcely audible but was complex and of two types. Type 1 squeaks lasted 0.08 to 0.14 s with a fundamental frequency of 1,700 to 2,500 Hz. Type 2 squeaks lasted 0.11 to 0.14 s with a fundamental frequency of 12,000 to 24,000 Hz. Harmonics at 70,000 Hz possibly are present. (The true channel of communication may be ultrasonic.) This cry waned at age 16 to 17 days. Neonates made comfort sounds (low, rapid peeps) while being groomed by the female.

When startled, canyon mice rarely displayed foot-pattering but usually exhibited tooth-chattering during aggressive arousal. Mice responded to bites or injuries with squeaks. The warning squeak or "chit" given during nest defense occurred in bursts of one to 10 with each squeak lasting 0.04 to 0.05 s at a fundamental frequency of 3,600 to 21,000 Hz (Eisenberg, 1968).

Captive canyon mice are remarkably agile (Egoscue, 1964). Individuals missing half or more of the tail were unable to perform some of the complicated leaps and climbs characteristic of captive canyon mice. King et al. (1968) found that canyon mice were significantly better climbers and runners, above average diggers, and average swimmers and gnawers compared to several other species of *Peromyscus*.

Lemen (1980) showed a general association between navigating through a structurally complex habitat and a relatively large brain for 12 species of *Peromyscus*. However, canyon mice do not follow the usual trend; they inhabit complex habitats but have small brains relative to body size and length of tail.

Canyon mice sandbathe to remove oil from their long pelage; in the absence of sand or fine soil, the coat becomes oily and matted (King et al., 1968).

GENETICS. Brown and Welser (1968) reported that serum albumins of canyon mice from Colorado and California were the same and both populations were monomorphic. Jensen and Rasmussen (1971) described two albumins in canyon mice from Utah, both of which were similar to some albumins of *P. maniculatus* and *P. leucopus*. Zimmerman et al. (1978) studied allelic variation at 23 loci in 14 nominal species of *Peromyscus*, and indicated that *P. crinitus* clustered with *P. maniculatus*.

By contrast with a general paucity of information on transmissional and biochemical genetics, cytogenetic study of *P. crinitus* has been extensive. As in all other members of the genus, the diploid number is 48 (Hsu and Arrighi, 1968). The autosomal complement has 20 pairs of acrocentric chromosomes and 3 pairs of biarmed chromosomes (a large submetacentric pair, a small biarmed pair, and a smaller, nearly metacentric pair). The X chromosome is submetacentric and the Y chromosome varies from metacentric to submetacentric.

Pathak et al. (1973) and Clark et al. (1973) reported C-banded chromosomes from *P. crinitus* and *P. eremicus*. *P. crinitus* has only eight heterochromatic arms (FN = 56), whereas *P. eremicus* has 40 heterochromatic arms (FN = 96). Total length of metaphase chromosomes in the canyon mouse is 123.2 ± 8.5 μ; total length of euchromatin is 115.9 ± 9.42 μ. Positive C-bands appear only at centromeres and on short arms of the three pairs of biarmed autosomes and the X chromosomes (Arrighi, 1975; Arrighi et al., 1976).

On the basis of comparisons of heterochromatin, satellite DNA, constitutive heterochromatin, ribosomal cistrons, and neutral CsCl bouyant density gradients of DNA, Hazen (1978) and Hazen and Arrighi (1978) questioned the placement of *P. crinitus* in the subgenus *Haplomylomys*, substantiating conclusions of earlier authors from comparative gross morphology.

The karyotype of *P. crinitus* is the simplest known in the genus (2n = 48, FN = 56). Hence, it has been taken to be primitive (Greenbaum and Baker, 1978; Robbins and Baker, 1981; Stangl and Baker, 1984) therefore useful in comparative and systematic studies within the genus *Peromyscus* and between *Peromyscus* and other genera (Baker et al., 1979; Mascarello et al., 1974; Yates et al., 1979).

Kuo (1979) demonstrated by nuclease digestion and two-dimensional gel electrophoresis that nucleosomal DNA from three species of *Peromyscus* (*P. eremicus*, *P. crinitus*, *P. collatus*) was similar. Deaven et al. (1977) used flow microfluorometric measurements of DNA to demonstrate that the genome of *P. eremicus* was 36% larger than that of *P. crinitus* because of an abundance of heterochromatin, thus substantiating earlier measurements of intact chromosomes. Because *P. crinitus* and *P. eremicus* have nearly identical euchromatin, but *P. crinitus* has one-third less heterochromatin than *P. eremicus*, the species have been used as extremes in comparative studies of chromosomal function. The rate of histone f2a2 phosphorylation in cells of *P. eremicus* was 1.5 to 2.0 times that in *P. crinitus*, whereas the rate of histone f1 phosphorylation was identical in cells of the two species, indicating that phosphorylation of histone f2a2 is involved in some aspect of heterochromatin function (Gurley and Walters, 1976; Gurley et al., 1978*a*, 1978*b*). Cultured cells of *P. eremicus* had proportionately more of the hydrophobic, more phosphorylated subfraction of heterochromatin than these of *P. crinitus*, suggesting that histones in the constitutive heterochromatin were relatively inaccessible to acetylation (Halleck and Gurley, 1979, 1980, 1981).

Lung cells of canyon mice in monolayer culture had the following characteristics: mass of DNA, 6.30×10^{-12} g; nuclear surface, 267 mm^2; nuclear volume, 153 mm^3; total pores, 3,116; nuclear pores/mm^2, 11.67 ($\pm SD$, 1.8); nuclear pores/mm^3, 20.4 (Maul and Deaven, 1977). *P. crinitus* differed significantly from *P. eremicus* only in nuclear volume and less DNA (Maul et al., 1980).

Because cell lines are available as in vitro cultures, *P. crinitus* has been used rather widely in biomedical studies, including studies of effects of Adriamycin (an antitumor antibiotic) on mitosis (Kusyk and Hsu, 1975), and survival after treatment with the mutagen 6-thioguanine (Basen and Hsu, 1977). In the absence of comparative data, general implications of such studies are not clear.

REMARKS. *Peromyscus crinitus* was included by Osgood (1909) as a member of the subgenus *Haplomylomys*, but he noted (p. 229): "*P. crinitus* is the most aberrant member in this group on account of its approach to the subgenus *Peromyscus* indicated by its molar teeth, but since it has only two pairs of mammae it seems best to include it here." Blair (1942) noted considerable differences in bacula within *Haplomylomys*, with *P. californicus* being unlike *P. crinitus* and *P. eremicus*. Hall and Hoffmeister (1942:51–52) wrote: "*P. crinitus* currently, and probably correctly, is placed in the subgenus *Haplomylomys* Osgood, but the presence of accessory cusps in the upper molars of some individuals, the presence of hairs on part of the sole of the hind foot, and some other features show the relationship of *crinitus* to the subgenus *Peromyscus* Gloger, and cause *P. crinitus* to be regarded as a species intermediate between the two subgenera or as an aberrant member of the subgenus *Haplomylomys*." Miller and Kellogg (1955) and Hall and Kelson (1959) listed *P. crinitus* in *Haplomylomys* without comment.

Hooper (1958) noted that the penis of *P. crinitus* is most like that of *P. maniculatus* or *P. polionotus*, albeit somewhat intermediate between the *maniculatus* and *boylei* "divisions" of the genus. Hooper (1958:12) concluded that "it clearly is unlike *eremicus* or *californicus*, the species with which it is currently grouped." Later, Hooper (1968, based on Hooper and Musser, 1964) and Carleton (1980) placed *crinitus* in the "*crinitus* group" (with *P. pseudocrinitus*) in the subgenus *Peromyscus*. On the basis of com-

parative morphology of the male reproductive glands, Linzey and Layne (1969) judged the canyon mouse to be intermediate between the *maniculatus* and *boylii* species groups. Lawlor (1971) used *P. crinitus* from Inyo Co., California, in an extensive taxonomic study of *Peromyscus* on islands in the northern part of the Gulf of California, and concluded that *P. crinitus* was more similar to *P. boylii* than to *P. eremicus* and its insular relatives. Hall (1981) placed the canyon mouse in the subgenus *Peromyscus*.

Stangl and Baker (1984) synthesized data from chromosomal, genic, and "classical" studies in a reappraisal of evolutionary relationships within *Peromyscus*. *P. crinitus* was arrayed in the "*crinitus* group" of the subgenus *Peromyscus*. Reviewing the ambiguous position of the *crinitus* group within the subgenus, they stressed the need for additional genic data on *P. crinitus* (and chromosomal and genic data on *P. pseudocrinitus*) to assess relationships within and among species groups and subgenera.

LITERATURE CITED

ABBOTT, K. D. 1971. Water economy in the canyon mouse *Peromyscus crinitus stephensi*. Comp. Biochem. Physiol., 38A: 37–52.

ALLEN, J. A. 1893. List of mammals collected by Mr. Charles P. Rowley in the San Juan Region of Colorado, New Mexico, and Utah, with descriptions of new species. Bull. Amer. Mus. Nat. Hist., 5:69–84.

ALLRED, D. M. 1956. Mites found on mice of the genus *Peromyscus* in Utah. Great Basin Nat., 16:23–31.

ALLRED, D. M., AND D E. BECK. 1966. Mites of Utah mammals. Sci. Bull., Brigham Young Univ., Biol. Ser., 8:1–123.

ARMSTRONG, D. M. 1972. Distribution of mammals in Colorado. Monogr., Univ. Kansas Mus. Nat. Hist., 3:1–415.

———. 1977. Distributional patterns of mammals in Utah. Great Basin Nat., 39:199–205.

———. 1979*a*. Distributional checklist of rodents of Canyonlands National Park, Utah. Occas. Papers Mus., Texas Tech Univ., 59:1–44.

———. 1979*b*. Ecological distribution of rodents in Canyonlands National Park, Utah. Great Basin Nat., 39:199–205.

———. 1982. Mammals of the Canyon Country. Canyonlands Nat. Hist. Assoc., Moab, Utah, 263 pp.

ARRIGHI, F. E. 1975. Genetic conservatism in phylogeny with special references to chromosomes. Pp. 200–207, *in* Mammalian cells: probes and problems (C. R. Richmond et al., eds.). Proc. Los Alamos Life Sci. Symp., 1:1–309.

ARRIGHI, F. W., A. D. STOCK, AND S. PATHAK. 1976. Chromosomes of *Peromyscus* (Rodentia, Cricetidae). V. Evidence of pericentric inversions. Chromosomes Today, 5:323–329.

BABERO, B. B., AND D. MATTHIAS. 1967. *Protospiura peromysci* n. sp. (Nematoda: Spiuridea) and other helminths from *Peromyscus* spp. in Nevada. J. Helminthol. Soc. Washington, 34: 255–261.

BAILEY, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna, 53:1–412.

BAKER, R. H. 1968. Habitats and distribution. Pp. 98–126, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.

BAKER, R. J., R. K. BARNETT, AND I. F. GREENBAUM. 1979. Chromosomal evolution in grasshopper mice (*Onychomys*: Cricetidae). J. Mamm., 60:297–306.

BANGS, O. 1899. Descriptions of some new mammals from western North America. Proc. New England Zool. Club, 1:67–72.

BASEN, B. M., AND T. C. HSU. 1977. Comparative mutagenicity and survival in two species of *Peromyscus* after selection in 6-thioguanine following induction with EMS and MNNG. Mamm. Chromosomes Newsl., 18:9.

BENSON, S. B. 1940. New subspecies of the canyon mouse (Peromyscus crinitus) from Sonora, Mexico. Proc. Biol. Soc. Washington, 53:1–4.

BLAIR, W. F. 1942. Systematic relationships of *Peromyscus* and several related genera as shown by the baculum. J. Mamm., 23:196–204.

BRADLEY, W. G., AND R. A. MAUER. 1973. Rodents of a creosote bush community in southern Nevada. Southwestern Nat., 17: 333–334.

BRANDT, D. H., AND J. L. KAVANAU. 1964. "Unrewarded" exploration and learning of complex mazes by wild and domestic mice. Nature, 204:267–269.

———. 1965. Exploration and movement patterns of the canyon mouse *Peromyscus crinitus* in an extensive laboratory enclosure. Ecology, 46:452–461.

BROWN, J. H., AND C. F. WELSER. 1968. Serum albumin polymorphisms in natural and laboratory populations of *Peromyscus*. J. Mamm., 49:420–426.

BURT, W. H. 1934. The mammals of southern Nevada. Trans. San Diego Soc. Nat. Hist., 7:375–427.

———. 1960. Bacula of North American mammals. Misc. Publ. Mus. Zool., Univ. Michigan, 113:1–76.

CARLETON, M. D. 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) with a reappraisal of the dichotomy within New World Cricetidae. Misc. Publ., Univ. Michigan Mus. Zool., 157:1–146.

CLARK, R. W., S. PATHAK, AND F. E. ARRIGHI. 1973. Similarities and dissimilarities of chromosomes and DNA in 2 species of deer mice (*Peromyscus*). J. Cell Biol., 59:57A.

COCKRUM, E. L. 1960. The Recent mammals of Arizona: their taxonomy and distribution. Univ. Arizona Press, Tucson, 276 pp.

DAVIS, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Caldwell, Idaho, 400 pp.

DEACON, J. E., W. G. BRADLEY, AND K. N. LARSEN. 1964. Ecological distribution of the mammals of Clark Canyon, Charleston Mountains, Nevada. J. Mamm., 45:397–409.

DEAVEN, L. L. ET AL. 1977. Chromosomes of *Peromyscus* (Rodentia, Cricetidae). Cytogenet. Cell Genet., 19:241–249.

DEWSBURY, D. A. 1975. Copulatory behavior of Peromyscus crinitus and Peromyscus floridanus. Amer. Midland Nat., 93: 468–471.

DEWSBURY, D. A., D. Q. ESTEP, AND D. L. LANIER. 1977. Estrous cycles of nine species of muroid rodents. J. Mamm., 58:89–92.

DICE, L. R. 1943. The biotic provinces of North America. Univ. Michigan Press, Ann Arbor, 78 pp.

DICE, L. R., AND P. M. BLOSSOM. 1937. Studies of mammalian ecology in southwestern North America with special attention to the colors of desert mammals. Publ. Carnegie Inst. Washington, 485:1–125.

DRICKAMER, L. C., AND B. M. VESTAL. 1973. Patterns of reproduction in a laboratory colony of *Peromyscus*. J. Mamm., 54: 523–528.

DUNMIRE, W. W. 1961. Breeding season of three rodents on White Mountain, California. J. Mamm., 42:489–493.

DURRANT, S. D. 1952. Mammals of Utah: taxonomy and distribution. Univ. Kansas Publ., Mus. Nat. Hist., 6:1–549.

EGOSCUE, H. J. 1964. Ecological notes and laboratory life history of the canyon mouse. J. Mamm., 45:387–396.

———. 1976. Flea exchange between deer mice and some associated small mammals in western Utah. Great Basin Nat., 36:475–480.

EIDEMILLER, B. J. 1980. Influence of competition on habitat use by desert omnivores. Amer. Zool., 20:953 (abstract only).

EISENBERG, J. F. 1963. The intraspecific social behavior of some cricetine rodents of the genus Peromyscus. Amer. Midland Nat., 69:240–246.

———. 1968. Behavior patterns. Pp. 451–495, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.

———. 1981. The mammalian radiations. An analysis of trends in evolution, adaptation, and behavior. Univ. Chicago Press, Chicago, 610 pp.

ELLIOT, D. G. 1904. Descriptions of twenty-seven apparently new species and subspecies of mammals. Field Columbian Mus. Publ., 87, Zool. Ser., 3:239–261.

FINDLEY, J. S., A. H. HARRIS, D. E. WILSON, AND C. JONES. 1975. Mammals of New Mexico. Univ. New Mexico Press, Albuquerque, 360 pp.

FISHER, J. L., AND S. P. CROSS. 1979. Battery light tracking as a technique for studying small nocturnal mammal movements. Northwest Sci., 53:90–93.

GOFF, M. L., AND R. B. LOOMIS. 1973. Two new species of *Odontacarus* (Acarina, Trombiculidae) from California and Baja California. J. Med. Entomol., 10:333–336.

GOLDMAN, E. A. 1932. Two new rodents from Arizona. Proc. Biol. Soc. Washington, 45:89–92.
———. 1937. The Colorado River as a barrier to mammalian distribution. J. Mamm., 18:427–435.
———. 1939. Nine new mammals from islands in Great Salt Lake, Utah. J. Mamm., 20:351–357.
GOIN, O. B. 1944. A new race of the canyon mouse. J. Mamm., 25:189–191.
GREENBAUM, I. F., AND R. J. BAKER. 1978. Determination of the primitive karyotype for *Peromyscus*. J. Mamm., 59:820–834.
GRUNDMANN, A. W. 1957. Nematode parasites of mammals of the Great Salt Lake Desert of Utah. J. Parasitol., 43:105–112.
GURLEY, L. R., AND R. A. WALTERS. 1976. Histone phosphorylation related to heterochromatin. J. Cell Biol., 70:153A.
GURLEY, L. R. ET AL. 1978*a*. Heterochromatin and histone phosphorylation. Exp. Cell. Res., 111:373–384.
———. 1978*b*. Involvement of histone phosphorylation in chromatin condensation. J. Supramolecular Structure, 7:321.
HAGMEIER, E. M. 1966. A numerical analysis of the distributional patterns of North American mammals, II. Re-evaluation of the provinces. Syst. Zool., 15:279–299.
HALL, E. R. 1946. Mammals of Nevada. Univ. California Press, Berkeley, 710 pp.
———. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 2:601–1181 + *90*.
HALL, E. R., AND D. F. HOFFMEISTER. 1942. Geographic variation in the canyon mouse, *Peromyscus maniculatus*. J. Mamm., 23:51–65.
HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. Ronald Press Company, New York, 2:547–1083 + *79*.
HALLECK, M. S., AND L. R. GURLEY. 1979. Histone acetylation and heterochromatin content of cultured Peromyscus cells. J. Cell Biol., 83:149A.
———. 1980. Histone modifications and heterochromatin content of cultured Peromyscus cells. Fed. Proc., 39:2008.
———. 1981. Histone acetylation and heterochromatin content of cultured Peromyscus cells. Exp. Cell. Res., 132:201–214.
HARDY, R. 1941. Dark coloration of some specimens of *Peromyscus crinitus*. J. Mamm., 22:90–91.
———. 1945. The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecol. Monogr., 15:71–108.
HARRIS, A. H. 1963. Ecological distribution of some vertebrates in the San Juan Basin, New Mexico. Papers Anthropol., Mus. New Mexico Press, 8:1–63.
———. 1970. The Dry Cave mammalian fauna and late Pluvial conditions in southeastern New Mexico. Texas J. Sci., 22:3–27.
HAYWARD, C. L., D. E. BECK, AND W. W. TANNER. 1958. Zoology of the Upper Colorado River Basin. I. The biotic communities. Brigham Young Univ. Sci. Bull., Biol. Ser., 1:1–74.
HAZEN, M. C. W. 1978. Cytological and molecular characterization of the genomes of four species of *Peromyscus*. Diss. Abstr. Internat. (B), 39:2620.
HAZEN, M. C. W., AND F. E. ARRIGHI. 1978. Genome analysis of four species of the genus *Peromyscus*. Mamm. Chromosomes Newsl., 20:25.
HOFFMEISTER, D. F., AND F. E. DURHAM. 1971. Mammals of the Arizona Strip including Grand Canyon National Monument. Tech. Ser., Mus. Northern Arizona, 11:1–44.
HOLBROOK, S. J. 1977. Rodent faunal turnover and prehistoric community stability in northwestern New Mexico. Amer. Nat., 111:1195–1208.
———. 1980. Species diversity patterns and prehistoric rodent communities. Oecologia, 44:355–367.
HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and Assoc. Syst. Coll., Lawrence, Kansas, 694 pp.
HONEYCUTT, R. L. ET AL. 1981. The influence of topography and vegetation on the distribution of small mammals in southwestern Utah, USA. Southwestern Nat., 26:295–300.
HOOPER, E. T. 1957. Dental patterns in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., Univ. Michigan, 99:1–59.
———. 1958. The male phallus in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., Univ. Michigan, 105:1–24.
———. 1968. Classification. Pp. 27–74, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.
HOOPER, E. T., AND G. G. MUSSER. 1964. Notes on classification of the rodent genus *Peromyscus*. Occas. Papers Mus. Zool., Univ. Michigan, 635:1–13.
HSU, T. C., AND F. E. ARRIGHI. 1968. Chromosomes of *Peromyscus* (Rodentia: Cricetidae). I. Evolutionary trends in 20 species. Cytogenetics, 7:417–446.
HUEY, L. M. 1931. A new subspecies of Peromyscus from the Gulf Coast of Lower California, Mexico. Trans. San Diego Soc. Nat. Hist., 6:389–390.
JENSEN, J. N., AND D. I. RASMUSSEN. 1971. Serum albumins in natural populations of *Peromyscus*. J. Mamm., 52:508–514.
JOHNSON, D. W. 1976. Populations of small mammals on isolated buttes in Canyonlands National Park, Utah. Unpubl. M.S. thesis, Univ. Wyoming, Laramie, 84 pp.
———. 1981. Ecology of small mammals on two isolated buttes in Canyonlands National Park, Utah. Southwestern Nat., 26: 395–407.
———. 1983. Ecology and biogeography of isolated butte communities on the Colorado Plateau. Unpubl. Ph.D. dissert., Univ. Colorado, Boulder, 203 pp.
———. 1986. Desert buttes: natural experiments for testing theories of island biogeography. Natl. Geogr. Res., 2:152–166.
JORGENSEN, C. D., AND C. L. HAYWARD. 1965. Mammals of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser., 6:1–81.
KAUFMAN, D. W., G. A. KAUFMAN, AND J. G. WIENER. 1975. Energy equivalents for 16 species of xeric rodents. J. Mamm., 56:946–949.
KAVANAU, J. L. 1963. Compulsory regime and control of environment in animal behavior. I. Wheel running. Behaviour, 20: 251–281.
———. 1967. Behavior of captive white-footed mice. Science, 155:1623–1639.
KAVANAU, J. L., AND R. M. HAVENHILL. 1976. Compulsory regime and control of environment in animal behavior, part 3. Light level preferences of small nocturnal mammals. Behaviour, 59: 203–225.
KELSON, K. R. 1951. Speciation in rodents of the Colorado River drainage. Biol. Ser., Univ. Utah, 11:1–125.
KENAGY, G. J., AND D. F. HOYT. 1980. Reingestion of feces in rodents and its daily rhythmicity. Oecologia, 44:403–409.
KING, J. A., E. O. PRICE, AND P. G. WEBER. 1968. Behavioral comparisons within the genus *Peromyscus*. Papers Michigan Acad. Sci., Arts, and Letters, 53:113–136.
KIRKLAND, G. L., JR. 1980. The zoogeography of the mammals of the Uinta Mountains. Southwestern Nat., 26:325–339.
KLINGENER, D. 1968. Anatomy. Pp. 127–147, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.
KUO, M. T. 1979. Studies in heterochromatin DNA accessibility of late replicating heterochromatin DNA in chromatin to micrococcal nuclease digestion. Chromosoma, 70:183–194.
KUSYK, C. J., AND T. C. HSU. 1975. Effects of Adriamycin on mammalian chromosomes in-vitro. Fed. Proc., 34:867.
LAWLOR, T. B. 1971. Evolution of *Peromyscus* on northern islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist., 16:91–124.
LAYNE, J. N. 1968. Ontogeny. Pp. 148–253 *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.
LEMEN, C. 1980. Relationship between relative brain size and climbing ability in *Peromyscus*. J. Mamm., 61:360–364.
LINZEY, A. V., AND J. N. LAYNE. 1969. Comparative morphology of the male reproductive tract in the rodent genus *Peromyscus* (Muridae). Amer. Mus. Novitates, 2355:1–47.
LONG, C. A. 1965. The mammals of Wyoming. Univ. Kansas Publ., Mus. Nat. Hist., 14:493–758.
MACMILLEN, R. E. 1972. Water economy of nocturnal desert rodents. Symp. Zool. Soc. London, 31:147–174.
———. 1983. Water regulation in *Peromyscus*. J. Mamm., 64: 38–47.
MACMILLEN, R. E., AND E. A. CHRISTOPHER. 1974. The water

relations of two populations of noncaptive desert rodents. Pp. 117–137, *in* Environmental physiology of desert organisms (N. F. Hadley, ed.). Halstead Press, New York, 283 pp.

MASCARELLO, J. T., A. D. STOCK, AND S. PATHAK. 1974. Conservatism in the arrangement of genetic material in rodents. J. Mamm., 55:695–704.

MATSON, J. O. 1976. The distribution of rodents in the Owens Lake Region, Inyo County, California. Contrib. Sci. Nat. Hist. Mus. Los Angeles Co., 276:1–27.

MAUL, G. G., AND L. L. DEAVEN. 1977. Quantitative determination of nuclear pore complexes in cycling cells with differing DNA content. J. Cell Biol., 73:748–760.

MAUL, G. G. ET AL. 1980. Investigation of the determinants of nuclear pore number. Cytogenet. Cell Genet., 26:175–190.

MCNAB, B. K. 1968. The influence of fat deposits on the basal rate of metabolism in desert homoiotherms. Comp. Biochem. Physiol., 26:337–343.

MCNAB, B. K., AND P. MORRISON. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecol. Monogr., 33:63–82.

MEARNS, E. A. 1897. Descriptions of six new mammals from North America. Proc. U.S. Nat. Mus., 19:719–724.

MERRIAM, C. H. 1891. Results of a biological reconnaissance of south-central Idaho. N. Amer. Fauna, 5:1–127.

MILLER, G. S., JR., AND R. KELLOGG. 1955. List of North American Recent mammals. Bull., U.S. Nat. Mus., 205:1–954.

MILLER, W. E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity exclusive of Rancho la Brea. Bull. Los Angeles Co. Mus. Nat. Hist., 10:1–124.

MODI, W. S. 1984. Reproductive tactics among deer mice of the genus *Peromyscus*. Canadian J. Zool., 62:2576–2581.

MORHARDT, J. E., AND J. W. HUDSON. 1966. Daily torpor induced in white-footed mice (*Peromyscus* spp.) by starvation. Nature, 212:1046–1047.

MORTON, S. R. 1979. Diversity of desert dwelling mammals: a comparison of Australia and North America. J. Mamm., 60: 253–264.

MULLEN, R. K. 1971. Energy metabolism of *Peromyscus crinitus* in its natural habitat. J. Mamm., 52:633–635.

NELSON, B. C., AND C. R. SMITH. 1976. Ecological effects of a plague epizootic on the activities of rodents inhabiting caves at Lava Beds National Monument, California. J. Med. Entomol., 13:51–61.

OSGOOD, W. H. 1909. Revision of the mice of the American genus Peromyscus. N. Amer. Fauna, 28:1–285.

PATHAK, S., T. C. HSU, AND F. E. ARRIGHI. 1973. Chromosomes of *Peromyscus* (Rodentia, Cricetidae) IV. The role of heterochromatin in karyotypic evolution. Cytogenet. Cell Genet., 12: 315–326.

PRESNALL, C. C. 1938. Mammals of Zion, Bryce, and Cedar Breaks. Zion and Bryce Mus. Bull., 2:1–20.

RIDGWAY, R. 1912. Color standards and color nomenclature. Privately published, Washington, D.C., 43 pp.

ROBBINS, L. W., AND R. J. BAKER. 1981. An assessment of the nature of chromosomal rearrangements in 18 species of *Peromyscus* (Rodentia: Cricetidae). Cytogenet. Cell Genet., 31: 194–202.

RUFFNER, G. A., N. J. CZAPLEWSKI, AND S. W. CAROTHERS. 1978. Distribution and natural history of some mammals from the inner gorge of the Grand Canyon, Arizona. J. Arizona-Nevada Acad. Sci., 13:85–91.

RYAN, R. M. 1968. Mammals of Deep Canyon, Colorado Desert, California. The Desert Museum, Palm Springs, California, 137 pp.

STANGL, F. B., JR., AND R. J. BAKER. 1984. Evolutionary relationships of *Peromyscus*: congruence of chromosomal, genic, and classical data sets. J. Mamm., 65:643–654.

STARK, H. E., AND A. R. KINNEY. 1969. Abundance of rodents and fleas as related to plague in Lava Beds National Monument, California. J. Med. Entomol., 6:287–294.

STUDIER, E. H. ET AL. 1977. Thermal sensitivity and activation energy of intrinsic intestinal motility in small vertebrates. J. Thermal Biol., 2:101–105.

SUMNER, F. B., AND H. S. SWARTH. 1924. Supposed effects of the color tone of the background upon the coat color of mammals. J. Mamm., 5:87–113.

TANNER, W. W. 1965. A comparative population study of small vertebrates in the uranium areas of the Upper Colorado River Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser., 7: 1–31.

THOMPSON, S. D. 1982. Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecology, 63:1313–1321.

WHITAKER, J. O., JR. 1968. Parasites. Pp. 254–311, *in* Biology of *Peromyscus* (Rodentia) (J. A. King, ed.). Spec. Publ., Amer. Soc. Mamm., 2:1–593.

WIENER, J. G. ET AL. 1977. Chemical composition of rodents: use of whole body concentrations for estimation of standing crops of elements. Southwestern Nat., 22:77–88.

YATES, R. L., R. J. BAKER, AND R. K. BARNETT. 1979. Phylogenetic analysis of karyological variation in three genera of peromyscine rodents. Syst. Zool., 28:40–48.

ZIMMERMAN, E. G., C. W. KILPATRICK, AND B. J. HART. 1978. The genetics of speciation in the rodent genus *Peromyscus*. Evolution, 32:565–579.

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