MAMMALIAN SPECIES 42(868):230–243

Microtus californicus (Rodentia: Cricetidae)

NICHOLE L. CUDWORTH AND JOHN L. KOPROWSKI

School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721, USA; ncudwo@gmail.com (NLC); squirrel@ag.arizona.edu (JLK)

Abstract: *Microtus californicus* (Peale, 1848) is a cricetid commonly called the California vole or California meadow mouse. A sexually dimorphic, medium-sized vole, *M. californicus* is 1 of 62 species in the genus *Microtus*. It is found in the interior valleys of southwestern Oregon, most of California, and northern Baja California, Mexico. *M. californicus* is found in a wide range of habitats from arid uplands to wet meadows and salt marshes. Several subspecies are listed as of conservation concern; the Amargosa vole, *M. c. scirpensis*, is listed as federally endangered. DOI: 10.1644/868.1.

Key words: arvicoline, California meadow mouse, California vole, cricetid, microtine, rodent

Synonymy completed 22 April 2008

www.mammalogy.org

Microtus californicus (Peale, 1848)
California Vole

Arvicola californica Peale, 1848:46. Type locality "Bay of San Francisco, in California;" restricted to San Francisquito Creek, near Palo Alto by Kellogg (1918:5).

Arvicola edax Le Conte, 1853:405. Type locality "California;" restricted to south of San Francisco by Bailey (1900:37).

Arvicola trowbridgii Baird, 1857:529. Type locality "Monterey," California; original description under *Arvicola montana*.

[*Microtus*] *californicus*: Trouessart, 1897:563. First use of current name combination.

Microtus scirpensis Bailey, 1900:38. Type locality "Amargosa River (near Nevada line), Inyo County, Calif[ornia]."

M. c. neglectus Kellogg, 1918:31. Type locality "Escondido, 640 feet altitude, San Diego County, California."

M. c. perplexabilis Grinnell, 1926:223–224. Type locality "La Grulla, 7000 feet altitude, Sierra San Pedro Martir, Lower California."

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Arvicolinae, tribe Arvicolini (Musser and Carleton 2005). *M. californicus* is 1 of 62 species in the genus *Microtus*; earlier work placed *M. californicus* in the subgenus *Microtus* (Hall 1981) but more recently it has been placed in the subgenus *Mynomes* (Zagorodnyuk 1990). Seventeen subspecies of *M. californicus* are recognized (Hall 1981):

M. c. aequivocatus Osgood, 1928:56: Type locality "San Quintin, [Baja] California."

M. c. aestuarinus: Kellogg, 1918:15. Type locality "Grizzly Island, Solano County, California."

M. c. californicus (Peale, 1848:46). See above; *edax* Le Conte and *trowbridgii* Baird are synonyms.

M. c. constrictus Bailey, 1900:36. Type locality "Cape Mendocino, [Humboldt Co.,] California."

M. c. eximius Kellogg, 1918:12. Type locality "Lierly's Ranch, 2,340 feet altitude, 4 miles south of Mount Sanhedrin, Mendocino County, California."

M. c. grinnelli Huey, 1931:47. Type locality "Sangre de Cristo in Balle San Rafael on the western base of the

Fig. 1.—A subadult *Microtus californicus* from Richmond Field Station, Contra Costa County, California, 3 June 1994. Used with permission of the photographer W. Z. Lidicker.

Sierra Juárez, [Baja] California, Mexico, lat. 31° 52′ north, log. 116° 06′ west."

M. c. halophilus Von Bloeker, 1937:156. Type locality "Moss Landing, Monterey County, California."

M. c. huperuthrus Elliot, 1903:161. Type locality "San Quentin, [Baja] California;" *perplexabilis* Grinnell is a synonym.

M. c. kernensis Kellogg, 1918:26. Type locality "Fay Creek, 4,100 feet altitude, Kern County, California."

M. c. mariposae Kellogg, 1918:19. Type locality "1.75 miles west of El Portal, 1,800 feet altitude, Mariposa County, California."

M. c. mohavensis Kellogg, 1918:29. Type locality "Victorville, 2,700 feet altitude, San Bernardino County, California."

M. c. paludicola Hatfield, 1935b:316. Type locality "Melrose Marsh, Alameda County, California."

M. c. sanctidiegi Kellogg, 1922:78. Replacement name for *M. c. neglectus* Kellogg, 1918.

M. c. sanpabloensis Thaeler, 1961:81. Type locality "San Pablo Creek (salt marsh), Contra Costa County, California."

M. c. scirpensis Bailey, 1900:38. See above.

M. c. stephensi Von Bloeker, 1932:134. Type locality "Playa del Rey, Los Angeles County, California."

M. c. vallicola Bailey, 1898:89. Type locality "Lone Pine, Inyo Co., California."

DIAGNOSIS

Microtus californicus (Fig. 1) may be sympatric with 6 other species of *Microtus* (Hall 1981). Six plantar tubules and side glands on hips of males distinguish *M. californicus* from the North American water vole (*M. richardsoni*) and the creeping vole (*M. oregoni*), each with 5 plantar tubules and side glands on flanks or inconspicuous side glands, respectively (Hall 1981). *M. californicus* can be distinguished from Townsend's vole (*M. townsendii*), the gray-tailed vole (*M. canicaudus*), and the montane vole (*M. montanus*) by the lack of abrupt constriction of the incisive foramen, which is narrower posteriorly than anteriorly. The long-tailed vole (*M. longicaudus*) has a longer tail measuring greater than one-third the body length (Hall 1981). *M. montanus* and *M. townsendii* tend to occupy different ranges, further separating these species (Ingles 1965).

GENERAL CHARACTERS

Microtus californicus is a medium-sized vole with light gray vibrissae, gray feet, and white near the anus (Verts and Carraway 1998). Dorsum is cinnamon-brown to tawny olive with dark brown to black hairs; venter fur is medium gray, occasionally washed with buff. Tail is bicolored, with black above and gray below (Verts and Carraway 1998). Subspecies inhabiting marsh lands (*M. c. aestuarinus*, *M. c. vallicola*, and *M. c. scirpensis*) tend to have a blackish dorsum; subspecies inhabiting the higher foothills (*M. c. huperuthrus*, *M. c. sanctidiegi*, and *M. c. mariposae*) are reddish (Kellogg 1918). *M. c. constrictus* is noticeably smaller (Kellogg 1918).

Microtus californicus demonstrates sexual dimorphism; males average 6% longer and 11% heavier than females (Heske and Ostfeld 1990). Means ± *SE* (mm; ranges) of external and cranial measurements (Fig. 2) of *M. c. eximius* in Oregon for 19 males and 21 females, respectively, were: total length, 174.0 ± 2.9 (152–196), 167.0 ± 2.0 (149–182); length of tail, 49.0 ± 1.2 (42–58), 45.0 ± 0.9 (38–53); length of hind foot, 22.0 ± 3.8 (21–24), 22.0 ± 0.3 (18–23); occipitonasal length, 28.49 ± 0.27 (26.18–30.72), 28.13 ± 0.23 (26.42–30.19); basal length, 26.95 ± 0.35 (23.94–29.87), 26.39 ± 0.22 (24.62–28.21); length of nasals, 9.31 ± 0.16 (8.11–10.40), 9.14 ± 0.11 (8.12–9.97); length of incisive foramen, 5.61 ± 0.11 (4.89–6.65), 5.61 ± 0.06 (4.96–6.11); length of maxillary toothrow, 7.24 ± 0.09 (6.73–7.90), 7.24 ± 0.07 (6.47–7.62); zygomatic breadth, 16.78 ± 0.18 (15.26–18.00), 16.54 ± 0.17 (15.24–18.28); braincase breadth, 11.38 ± 0.11 (10.64–12.59), 11.32 ± 0.13 (10.04–12.09); least interorbital length, 3.72 ± 0.04 (3.41–4.01), 3.66 ± 0.05 (3.35–4.11); and skull depth, 10.58 ± 0.07 (10.10–11.07), 10.31 ± 0.07 (9.77–11.02—Verts and Carraway 1998). Means ± *SE* (g; range) of body mass of *M. c. eximius* in Oregon for 9 males and 9 females, respectively, were 47.1 (41.4–54.5) and 43.4 ± 1.79 (36.0–55.2—Verts and Carraway 1998).

Size may vary considerably across the range, with several southern subspecies larger than more northerly subspecies (Heske and Lidicker 1999); means ± *SE* (mm) of body length of *M. c. aestuarinus* in central California for 15 males and 16 females, respectively, were 142.2 ± 4.9 and 135.9 ± 5.1 (Heske and Ostfeld 1990). Both cyclic and noncyclic populations may exhibit extralarge individuals during years providing good conditions for growth and survival, up to 80.9 g and 62.5 g for males and females, respectively (Lidicker and Ostfeld 1991).

DISTRIBUTION

Microtus californicus reaches a northern limit near Eugene, Oregon, and a southern limit near El Rosario, Baja California, Mexico (Verts and Carraway 1998; Fig. 3). In the United States, *M. californicus* is found in interior valleys in Oregon and most of California, but is absent from the northwestern fog belt, northeastern sagebrush region, and southeastern desert region of California (Verts and Carraway 1998). The nearly continuous range of *M. californicus* is punctuated with isolated subspecies in northern Baja California and the Mojave Desert, White Mountains, and Panamint Range in eastern California (Heske and Lidicker 1999).

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Microtus californicus* (UA [The University of Arizona mammal collection] 14224) from end Rock Oak Road, Walnut Creek, Contra Costa County, California. Occipitonasal length is 26 mm.

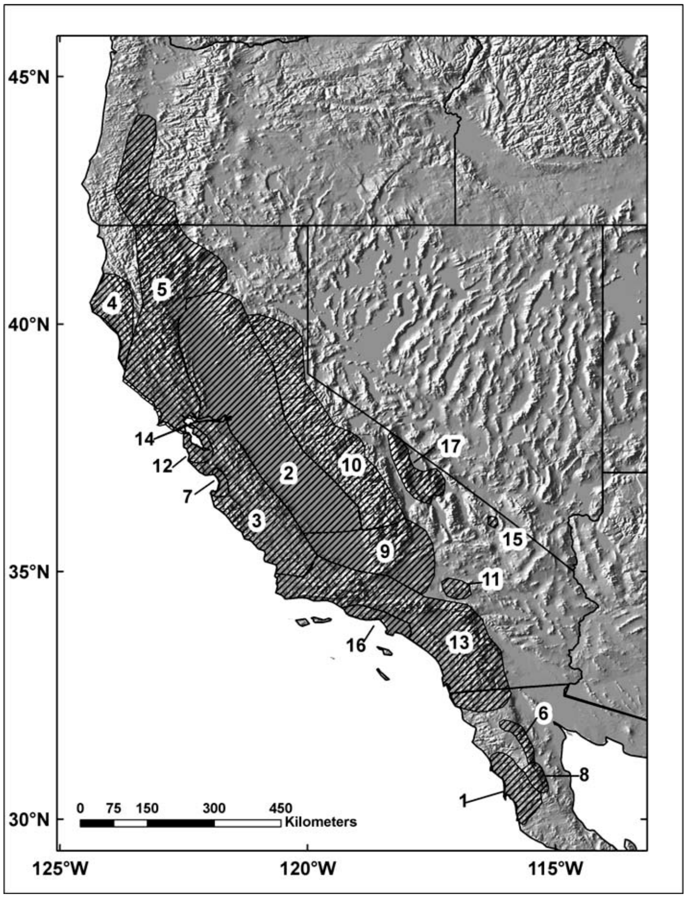

Fig. 3.—Geographic distribution of *Microtus californicus*. Subspecies are: 1, *M. c. aequivocatus*; 2, *M. c. aestuarinus*; 3, *M. c. californicus*; 4, *M. c. constrictus*; 5, *M. c. eximius*; 6, *M. c. grinnelli*; 7, *M. c. halophilus*; 8, *M. c. huperuthrus*; 9, *M. c. kernensis*; 10, *M. c. mariposae*; 11, *M. c. mohavensis*; 12, *M. c. paludicola*; 13, *M. c. sanctidiegi*; 14, *M. c. sanpabloensis*; 15, *M. c. scirpensis*; 16, *M. c. stephensi*; 17, *M. c. vallicola*. Map redrawn from Hall (1981) with modifications from Verts and Carraway (1998). Map created by M. Merrick.

FOSSIL RECORD

Microtus californicus is believed to have reached North America via immigration from Beringia (Repenning 1992); however, the 1st appearance of *M. californicus* in the fossil record is debated (Bell and Bever 2006; Hoffmann and Koeppl 1985). An edentulous dentary discovered from Vallecito Creek in the Anza-Borrego Desert, San Diego County, California, was tentatively assigned to *M. californicus* (Zakrzewski 1972) and can be dated to Irvingtonian (Kansan; about 1.2 million years ago—Zakrzewski 1985). Additional dental fossils place *M. californicus* in the Irvington fauna (Alameda County, California—Repenning 1987, 1992; Zakrzewski 1985) between 780,000 and 1.2 million years ago (Bell and Beaver 2006). Assignment to species status has since been disputed (Bell and Beaver 2006); however, the fossils remain among the oldest dated material for *Microtus* worldwide, an estimated 1.4 million years ago (Repenning 1992). *M. californicus* also was found in deposits in southern California closely overlaying the Olduvai Event of normal polarity, at least 1.8 million years ago (Repenning 1980).

Other fossils from California are Rancholabrean (Wisconsin; about 20,000 years ago) in age (specific ages, when available, based upon radiocarbon dating): Rancho La Brea, Los Angeles County (12,650 ± 160 to 40,000+ years ago); McKittrick, Kern County (38,000 ± 2,500 years ago); La Mirada, Los Angeles County (10,690 ± 360 years ago); Samwell Cave, Shasta County; Potter Creek Cave, Shasta County; Carpinteria, Santa Barbara County; San Pedro, Los Angeles County; Emery Borrow Pit, Los Angeles County; Zuma Creek, Los Angeles County; Costeau Pit, Orange County; Newport Bay Mesa, Orange County; and Kokoweef, San Bernadino County (Clements 1936; Zakrzewski 1985). Two records from Nevada, Tule Springs, Clark County, and Glendale, Clark County, also are Rancholabrean in age but are outside the current distribution of *M. californicus* (Zakrzewski 1985); the Glendale specimen may represent a misidentified *M. montanus* (Kurtén and Anderson 1980). No fossils have been discovered from Oregon (Verts and Carraway 1998).

FORM AND FUNCTION

Form.—Young *Microtus californicus* can be accurately aged to within 4 days based upon molt progression; molts are irregular and unreliable age indicators once adult pelage is reached at about 60 days (Ecke and Kinney 1956). Fur comprises 2.6% of adult vole body mass with longest hairs measuring 13.8 mm ± 0.6 *SD* (Kenagy and Pearson 2000). Skull characteristics tend to increase in size with age but decrease with respect to basilar length (Hatfield 1935a). Following eruption of M3 at 22 days, no further cranial characteristics are correlated with age (Ecke and Kinney 1956). Presence or absence of 3 skull foramina (preorbital, maxillary, and sphenoid) appears to have at least some genetic basis and may serve as a measure of genetic differences between local populations (Hilborn 1974). The skull lacks a pronounced median crest (Hall 1981).

Dental formula of *M. californicus* is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Fig. 2). Incisive foramina are rounded at both ends, widest in the middle, and not constricted posteriorly (Hall 1981). *M. californicus* displays 3 closed triangles and 1 open triangle on M2, 3 closed triangles on M3, 5 closed triangles on m1, 4 closed triangles on m2, and 3 transverse loops on m3 (Carleton 1985). Common variants are 4 closed triangles on M2, and 2 transverse loops and 2 open triangles on m3 (Carleton 1985). Anomalous individuals displaying abnormally long molar roots with dentine distortion at the root base have been observed in populations of *M. c. californicus* and *M. c. scirpensis* (Gill and Bolles 1982). The trait appears to have a genetic basis, but mode of inheritance is unknown; affected individuals do not demonstrate a difference in fitness from individuals with normal root length (Gill and Bolles 1982). Nasopalatine canals are open in adult *M. californicus*, the diastemal palate lacks the anterior longitudinal ridge, and inflexi of the upper lip are never fused (Quay 1954b). In 2 specimens, 44% of diastemal palate was anterior to the nasopalatine canal openings, and 55% of alveolobasilar length was formed by the diastemal palate. In a measure of the position of the incisive foramina for 19 specimens of *M. c. eximius*, percent ± *SD* of diastemal length anterior to the anterior tip of the incisive foramina was 32.7 ± 1.97, and percent of the diastemal length anterior to the posterior tip of the incisive foramina was 96.8 ± 1.83 (Quay 1954b).

Microtus californicus has 6 plantar tubercles (Hall 1981). The 4 pairs of mammae include 2 pectoral and 2 inguinal; males have a pair of glands located on the hips (Hall 1981). Average number ± *SD* (range) of meibomian glands in the eyelids for 10 specimens was: dorsal lid, 4.2 ± 0.9 (3–6); ventral lid 1.9 ± 0.9 (1–3); and both lids, 6.1 ± 1.4 (4–9—Quay 1954a). Number of glands was not correlated with sex, season, or age (Quay 1954a). Adrenal mass shows no consistent relationship to body mass (Mullen 1960). Right adrenal gland is typically smaller than left gland; paired adrenal mass ranges from 19.6 to 57.9 mg. Aberrant individuals may reach paired adrenal masses of 86.8–129.0 mg (Mullen 1960). The cecum of *M. californicus* is similar to that of the closely related red tree vole (*Arborimus* [formerly *Phenacomys*] *longicaudus*), measuring 65 mm long by 10–12 mm wide, but is without the postcecal spiral and cecal villi found in *A. longicaudus* (Voge and Bern 1949). Gastrointestinal length (± 2 *SE*) of 10 wild-caught individuals averaged 59.1 ± 37 mm, translating to a 4.93 ± 0.31 tract-to-body-length ratio (Bradley 1976). Average percentage of the tract (± 2 *SE*) composed of small intestine, cecum, and large intestine was 46.7% ± 0.93%, 21.9% ± 1.23%, and 31.4% ± 1.13%, respectively (Bradley 1976).

Bacular stalk is long and bowed upward at the end, 2.33 times greatest breadth and 4.5 times greatest depth, and greatest length is 3.0 mm (Anderson 1960). Base is rounded or slightly trilobed. Median process is ossified and is 0.25 length of stalk, basally broadened, and flattened and shallowly grooved ventrally; lateral processes are cartilaginous (Anderson 1960) and absent on preserved specimens (Anderson 1959; Hooper and Hart 1962). Bacular shaft is curved, terminally inflated dorsally, and slender and tapering from midpoint. Tuberosities are moderately developed and comparatively shallow with a median constriction of 0.8 at greatest depth, and concavity is slightly deeper and narrower dorsally than ventrally (Anderson 1960). Bacula of 2 juvenile males measured at 5 and 10 days old were 0.93 mm long by 0.29 mm wide, and 1.50 mm long by 0.57 mm wide, respectively (Ziegler 1961).

Dorsal lobe of glans penis is well differentiated with 4–6 papillae on rim and 8 or 9 distinct fingers per side (Hooper and Hart 1962). Dorsal papilla is wide-coned with only a distal spine, and medial mound is clearly separated from long bacular mounds. Urethral process has 3 unequal lobes, lacks lateral hooking, and is broader than long. Mean measurements from 2 specimens were: length, 3.8 mm and diameter, 2.4 mm (Hooper and Hart 1962). Female *M. californicus* demonstrate sporadic occurrence of a baubellum (os clitoridis—Ziegler 1961). Of 20 individuals examined, 2 had traces of a baubellum: a 15-day-old female had a club-shaped baubellum measuring 0.55 mm long, 0.6 mm wide, and 0.14 mm thick at the proximal end; a 58-day-old female had a fragment of a baubellum measuring about 0.05 mm long by 0.05 mm wide. The baubellum was not uniform in shape and was not present in any of the female littermates of either female (Ziegler 1961).

Function.—Standard metabolic rate (cc O_2 $g^{-1}\cdot h^{-1}$ ± 2 *SE*) of *Microtus californicus* is 1.15 ± 0.07, higher than expected based upon weight alone (Bradley 1976). *M. californicus* demonstrates no difference in metabolic rates during day versus night. When standardized to 20°C, minimum metabolic rate averaged 2.37 cc O_2 $g^{-1}\cdot h^{-1}$. Fifteen captive individuals maintained a mean body temperature (± 2 *SE*) of 38.8°C ± 0.18°C. Evaporative cooling accounted for 11.6% of weight loss (Bradley 1976). Thermal conductance of captive individuals (cc O_2 $g^{-1}\cdot h^{-1}\cdot C$ ± 2 *SE*) averaged 0.138 ± 0.015 (Bradley 1976). Individuals shaved during winter months (January to early March) demonstrated decreased survival as the season progressed, a higher daily energy expenditure than unshaved individuals (109.2 kJ/day and 96.6 kJ/day, respectively), and behavioral shifts including increased huddling and minimizing time spent above ground (Kenagy and Pearson 2000).

Microtus californicus with unrestricted water availability had a daily water consumption estimate of 25% of body mass, similar to water requirements of other vole species (Church 1966). Main reaction to water restriction was mass loss; restriction did not result in tissue dehydration or impairment of locomotion or other activities. Average mass (± *SE*) stabilized at 78.8% ± 1.1% of normal body mass after about 13 days for individuals restricted to 0.67 normal water uptake and 69.8% ± 1.4% of normal body mass after about 36 days for individuals restricted to 0.33 normal water uptake. Individuals survived an average of 5.6 days with complete water deprivation and displayed an average mass loss of 28.9%. Evaporative loss remained similar despite treatment (average range: 0.916–1.06 mg water loss per ml oxygen consumed), and no reduction in pulmocutaneous water loss was observed among treatments. Water-restricted individuals demonstrated reduced urinary–fecal water loss and consumed an average of 17% less food to maintain a similar food-to-water intake. Individuals maintained a constant body-water-to-solids ratio independent of treatment and demonstrated a negative relationship between body fat and water privation. Therefore, *M. californicus* may be able to tolerate significant short-term water deprivation, but demonstrates no long-term physiological adaptations to water deprivation (Church 1966).

In a captive population, *M. c. aestuarinus* consumed approximately 85% of body mass in fresh food daily, about 9.8 g and 7.6 g dry mass of alfalfa (*Medicago sativa*) or wild oats (*Avena fatua*), respectively (Jameson 1958). *M. californicus* is able to digest about half the energy available in bromegrass (*Bromus rigidus*) stems and leaves and 73% of the energy of annual ryegrass (*Lolium multiflorum*—Batzli and Cole 1979). Grass seeds comprise most of the summer diet, and increases in energy digested were offset by decreases in dry matter ingested (Batzli and Cole 1979). Daily energy budgets (kcal/day) of captive individuals were 20.44, 19.89, and 21.98 for winter, summer exclusive of reproduction, and summer inclusive of reproduction, respectively (Bradley 1976). Daily food intakes (± 2 *SE*) were estimated at 5.65 ± 0.49 g or 25,699 ± 2,163 calories, translating to 661 ± 57 calories per g body mass; daily feces output was 1.39 ± 0.13 g or 5,590 ± 509 calories, translating to 144.2 ± 12.8 calories per g body mass or 4,031 ± 116 calories per g feces. Total energy use per day averaged 20,036 ± 1,739 calories or 517 ± 45 calories per g body mass. Therefore, *M. californicus* has an estimated assimilation efficiency of 77.4% ± 1.5% (range: 74.4–78.7%—Bradley 1976).

An experimental population of *M. californicus* demonstrated no relationship between adrenocortical activity and population density (Houlihan 1963). However, voles had significantly lower thyroid activity and liver-glycogen stores following an experimental severe reduction in population size (i.e., crash). Blood nonprotein nitrogen increased during the crash and remained high for months after population stabilization (Houlihan 1963).

ONTOGENY AND REPRODUCTION

Ontogeny.—Neonates are born blind, deaf, and without fur or pigment (Verts and Carraway 1998); however, young *Microtus californicus* are sensitive to light before their eyes open (Hatfield 1935a). Juveniles do not respond to auditory cues until 7–8 days in the laboratory, but may respond as early as 5 days in the wild (Hatfield 1935a). Average body mass at birth is 2.8 g (Hatfield 1935a); laboratory-reared pups gain 1.12 g/day up to 30 days of age, when growth rate begins to decline (Selle 1928). Eyes begin to open at 9 days of age (Selle 1928). After eruption of M3 at 22 days of age, no further age-dependent changes to the skull are observed (Ecke and Kinney 1956). *M. californicus* uniquely molts from juvenile to adult, attaining juvenile pelage by day 5, postjuvenile pelage by week 3, and adult pelage by week 8 or 9 (Hatfield 1935a). This molt progression was expanded upon by Ecke and Kinney (1956), and was 88% accurate in aging 17- to 60-day-old *M. californicus* within 4 days. Juveniles display slower growth and reproductive maturation when housed with siblings than with nonsiblings, perhaps due to release of an unknown pheromone, because isolated individuals connected only by air supply still displayed suppressed growth (Batzli et al. 1977). Body mass at weaning is negatively correlated with litter size (Krohne 1981). Young are weaned after 2 weeks (Greenwald 1957) but will continue suckling up to 3 weeks if allowed (Hatfield 1935a). Minimum estimate of nestling mortality, not including entire litter loss, was 32%, and early juvenile mortality ranged from 0% to 82% (Hoffmann 1958).

Females may reproduce as early as 3 weeks of age; males require up to 6 weeks to reach sexual maturity (Hatfield 1935a). Sexual maturity for females and males is reached at 25–30 g and 35–40 g, respectively (Hoffmann 1958). A 10-g wild-caught female demonstrated reproductive activity (Greenwald 1956), although precocious breeding is rare and not observed for wild-caught males (Greenwald 1957). Females may undergo a sterile cycle at puberty (usually when <30 g), perhaps as a result of a hormone imbalance (Greenwald 1956). Males exposed to bedding from family members may demonstrate delayed development (Rissman and Johnston 1985), and females housed with littermates delay reproduction until mated with a strange male, possibly functioning to encourage dispersal and reduce inbreeding (Batzli et al. 1977). Reproductively undeveloped males are less effective at activating reproductive growth of females, suggesting male androgen may be an important stimulus in female reproductive growth (Rissman and Johnston 1985). Fertile males typically have a testes length > 6 mm (Greenwald 1957).

Reproduction.—Breeding season of *Microtus californicus* is not sharply defined, ranging from 270 to 320 days in length (Hoffmann 1958). Although *M. californicus* can breed year-round, reproduction is typically restricted in Mediterranean-type climates to the wet season between mid-September and late May or early June (Batzli and Pitelka 1971; Heske et al. 1984; Lidicker 1973, 1976). Proportion of pregnant females peaks midseason, between March and April (Greenwald 1957; Hoffmann 1958), and individuals born early in the year are capable of breeding during the same season (Greenwald 1957). Subadult males attain nonbreeding condition 6–12 weeks before adult males (Krebs 1966).

The onset of reproduction each year is likely determined by an interaction between environmental and social cues. Gonad weights of males are depressed with short photoperiods, lack of fresh green vegetation, and limited access to water (Nelson et al. 1983). However, inhibitory effects of short photoperiod can be overridden by ingestion of green vegetation in the laboratory (Nelson et al. 1983). In the field, young voles may be detected as early as 6 weeks after the 1st major rainfall in autumn but may show a delay of up to 5 months (Lidicker 1973). Declining populations tend to demonstrate a delay in the onset of breeding seasons; increasing populations contain a higher proportion of scrotal males and perforate females (Krebs 1966). The termination of breeding season is likely influenced by a reduction in available water (Lidicker 1976; Nelson et al. 1983), and breeding season can extend through the dry season if sufficient green vegetation is supplied (Lidicker 1976).

Ovulation is induced by copulation and occurs less than 15 h after mating (Greenwald 1956). Females can achieve pregnancy following a single round of copulation; however, likelihood of pregnancy increases with continued copulation (Kenney et al. 1979). Males can ejaculate on 1st mount (Kenney et al. 1979), although copulation may last up to 0.5 h with repeated matings (Hatfield 1935a). *M. californicus* produces a copulatory plug but does not exhibit a locking mechanism on the penis (Kenney et al. 1979).

Follicular diameter enlarges from 600 to 900 μm following copulation (Greenwald 1956). Copora lutea are maintained given ovulation is induced (Kenney et al. 1979). Number of corpora lutea often exceeds embryo count due to accessory corpora lutea (Greenwald 1956). Mean number of corpora lutea is 9.23 (Greeenwald 1957); average number of corpora lutea in an island population of *M. californicus* was 13.12, although up to 50 corpora lutea have been reported (Lidicker 1973). Fertilization occurs in upper portion of oviduct (Greenwald 1956). Ovulation rate and preimplantation loss cannot be reliably measured by number of corpora lutea because of occurrence of accessory corpora lutea (Hoffmann 1958), although lower ovulation rates between June and November were speculated (Lidicker 1973). Postimplantation embryo mortality in a wild population was 3.92% (Hoffmann 1958). An island population demonstrated 4.66% embryo reabsorption, with higher reabsorption, lower implantation, and fewer corpora lutea in the left uterine horn (Lidicker 1973); Greenwald (1957) found >7% of embryos reabsorbing in captured females. Pheromones from unfamiliar males may induce abortion by females in early pregnancy (Heske 1987a), and females on low-calcium diets experience poor reproduction (Batzli et al. 1980).

Gestation is 3 weeks (Hatfield 1935a; Hoffmann 1958). *M. californicus* exhibits postpartum estrus that may last for several days (Greenwald 1956); females can be receptive to mating as soon as 15 h after giving birth (Ingles 1965). Hoffmann (1958) measured incidence of postpartum breeding at 18.8%, but estimated a rate as high as 30%. Litter sizes vary geographically, seasonally, and with female age (Batzli and Pitelka 1971; Hoffmann 1958). Ovulation and litter size are inversely related to population density (Hoffmann 1958). However, no correlation was found between litter size and female mass, length, current age, or age at 1st reproduction; litter size tended to be consistent among females (Krohne 1981). Mean litter sizes have been reported as 4.20 (range 1–9 embryos—Greenwald 1956, 1957), 4.70 (range 2–9 young—Lidicker 1979), 4.94 (range 1–10 embryos—Hoffmann 1958), and 5.05 (Lidicker 1973). Litter size (± *SE*) was larger in an annual grassland than a perennial grassland, 5.23 ± 0.33 (range 1–10) and 3.42 ± 0.32 (range

1–10), respectively (Krohne 1980). Litter size reaches a peak mid–breeding season, and is larger for multiparous than primiparous females (5.19 ± 0.34 and 4.61 ± 0.25 young/litter, respectively—Hoffmann 1958). Longer breeding seasons may allow for increased numbers of litters per female but may be offset by reduced litter size (Greenwald 1957). In a laboratory setting, 7 mated pairs produced an average of 6.0 litters per pair and 4.7 young per litter (range 1–9 young) over 185 days (Colvin and Colvin 1970). Laboratory-reared *M. californicus* demonstrated a low heritability of litter size of 0.170 ± 0.024 *SE* (Krohne 1981).

ECOLOGY

Population characteristics.—*Microtus californicus* densities vary regionally, with some populations displaying relatively stable densities (Ostfeld and Klosterman 1986) and populations in seasonal habitats demonstrating cyclic patterns peaking every 3–5 years (Garsd and Howard 1981). Peak densities (individuals/ha) have been recorded at 371–395 (Batzli and Pitelka 1971), 309–494 (Pearson 1966), 618 (Batzli 1968), 247–1,149 (Krebs 1966), and 1,185 (Heske 1987b). *M. californicus* may become locally extinct during times of population lows (Ford and Pitelka 1984), and areas dominated by perennial grasslands may serve as refuges during population lows (Batzli 1974; Ostfeld et al. 1985). Both predation (Pearson 1966, 1971) and nutritional requirements (Batzli and Pitelka 1971; Ford and Pitelka 1984) have received support for explaining timing and intensity of density variations. Noncyclic populations, for example, in coastal regions, may maintain densities near 100 individuals/ha (Ostfeld and Klosterman 1986), although annual fluctuations peaking in winter and spring are still observed (Batzli and Pitelka 1971).

The longest recorded life span of a marked vole was 14 weeks in a camera-trapping study (Pearson 1960). A population in Sonoma County, California demonstrated an estimated weekly survival of 0.75 (Krohne 1982). Juveniles have fairly high survival until June or July, at which point mortality increases, peaking during dry summer months (Lidicker 1973); survival tends to be highest at the start and lowest at the termination of the breeding season (Batzli and Pitelka 1971). Sex ratios vary seasonally, but numbers of males and females are not different (Heske 1987b; Lidicker 1973); however, operational sex ratios tend to be female-biased (Heske 1987b), and female-biased sex ratios are common during the breeding season (Batzli and Pitelka 1971; Greenwald 1957; Lidicker 1973) and times of high population density (Heske 1987b; Ostfeld and Klosterman 1986; Ostfeld et al. 1985). Populations of *M. californicus* can quickly occupy and expand in unoccupied, suitable areas: estimated mean rates of increase were 0.08–2.14 during the early expansion phase of colonization following immigration from the mainland to Brooks Island, California (Lidicker and Anderson 1962).

Space use.—Home-range size varies with season and density and averages 68 m^2 and 103 m^2 for females and males, respectively, with male home ranges often overlapping entire female home ranges (Heske 1987b). Batzli (1968) estimated home-range size as 159.10–297.29 m^2 based upon track indices; Pearson (1960) estimated that individuals remained within a 15-m radius from the home burrow and likely spent the majority of time within a 5-m radius of the burrow. Core home-range sizes are similar between sexes, but males have significantly larger home ranges overall, with extensive overlap of female home ranges (1–5 female ranges) and little to no overlap of male home ranges (Heske 1987b; Ostfeld 1986); females demonstrate a bimodal pattern of intrasexual overlap with either high or low overlap of other females (Heske 1987b). *Microtus californicus* moves shorter distances overall during nonbreeding seasons, adult males move longer distances during breeding seasons than females and subadult males, and subadult females demonstrate more movement than adult females (Batzli and Pitelka 1971; Krebs 1966). Density and movement may be negatively correlated (Krebs 1966; but see Batzli and Pitelka 1971). Movements by females begin to increase in July and peak in January; movements by males peak at the onset of the breeding season (February) and again in October (Lidicker 1973). Dispersal to moist areas with more available vegetation may increase during warm, dry summers (Greenwald 1957). Breeding adults and nestlings are least likely to disperse, although all age classes are known to disperse (Heske 1987b).

Microtus californicus is commonly associated with graminoids, but may be found in a wide range of habitats, including grasslands with considerable forbs and short, woody shrubs, marshy areas with standing water, coastal-area salt marshes, well-drained, arid uplands, and oak savannah (Gardner 1917; Getz 1985; Heske and Lidicker 1999). *M. californicus* demonstrates a preference for perennial grasslands (dominated by *Elymus cinereus*) over those dominated by a common annual (*Bromus rigidus*—Batzli 1974). Krebs (1966) provides a list of 24 dominant grass, herb, and shrub species in a grassland inhabited by *M. californicus* in the San Francisco Bay area. In Baja California, *M. californicus* is most commonly associated with wet meadows from sea level to montane meadows in the Sierra San Pedro de Martir (Huey 1964). *M. californicus* occupies habitats with a wide range of soil moisture conditions (Getz 1985) and temperature and humidity extremes, with *M. c. aestuarinus* almost semiaquatic (Kellogg 1918).

Microtus californicus is primarily fossorial, coming above ground only to feed, urinate, and defecate (Pearson 1960). Aboveground runways connect entrances to burrows dug by voles, entrances to abandoned gopher (*Thomomys*) tunnels, or refuges under objects such as large boards. Runway use is typically restricted to a single family group, with little interchange of individuals among runways. The number of voles using a runway does not increase with increased density; *M. californicus* instead increases the number of active runways. An individual averaged 7.8 passages per runway in a 24-h period, and excursions averaged 7 min during daylight and 1 min during night. Average amount of time between daylight excursions is 1.7 h. *M. californicus* displays shorter and fewer aboveground excursions during night, except in dry summer months when excursions are more concentrated during early morning, perhaps to gather dew in response to moisture deprivation (Pearson 1960).

Ball-shaped nests of cut grass, measuring up to 25 cm in diameter, are constructed either in underground burrows (in dry, loose soil 7–15 cm below the surface) or in shallow depressions (commonly in rush [*Juncus*] clumps) above ground (Stark 1963). Many trails may lead to a single nest, but nests typically have only 1 opening. Mean nest weight is 98 g (range, 9–290 g); belowground nests tend to be heavier, and winter nests tend to be heavier and larger. Nest temperature is similar to soil temperature year-round, but may range between 7°C and 24°C between periods of occupation. *M. californicus* will eject nests from the site if they become too wet (Stark 1963). Males assist females in nest building in the laboratory at 15–18 days into pregnancy (Hatfield 1935a). Burrows are between 1.52 and 12.19 m long and typically have 3 or 4 divisions; *M. californicus* is known to construct blind burrows (Stark 1963).

Diet.—*Microtus californicus* forages on grasses, sedges, and forbs, and subsists primarily on seeds and roots during the dry summer season (Batzli and Pitelka 1971), although green vegetation is necessary for reproduction (Nelson et al. 1983). Field data indicate *Avena fatua*, *Lolium multiflorum*, and *B. rigidus*, all introduced species, are the most preferred food items (Batzli and Pitelka 1971). In a laboratory preference test, *M. californicus* preferred grasses over forbs (although *Picris echinoids* also was preferred); grass seed heads and upper stems were preferred to lower stems (Gill 1977a). Preferred grasses were *Hordeum stebbinsii*, *Bromus racemosa*, and *Lolium perenne*; preferred forbs were *Plantago lanceolata* and *P. echinoids*, partially supporting field data because similar species were occasionally used in place of available wild species (Gill 1977a). Insects and fungi have not been reported from stomach contents of *M. californicus* (Batzli and Pitelka 1971).

Diseases and parasites.—*Microtus californicus* is a known carrier of both Sin Nombre *Hantavirus* (*Bunyaviridae*) and Isla Vista virus, a genetically distinct *Hantavirus* species, with prevalences of 12.5% and 15.0%, respectively (Bennett et al. 1999; Song et al. 1995). *M. californicus* may serve as a reservoir for plague (*Yersinia pestis*—Allred 1952; Kartman et al. 1962); Quan and Kartman (1962) classified *M. californicus* as "highly resistant" to the disease, but populations may be more than 3 times more susceptible when not previously exposed. Other recorded diseases include granulocytic anaplasmosis (*Anaplasma phagocytophilum*), tularemia (*Francisella tularensis*—Nieto et al. 2007), a type of orthopoxvirus (Regnery 1987), and Lyme disease (*Borrelia burgdorferi*—Peavey et al. 1997; Vredevoe et al. 2004). *M. californicus* carries *Pneumocystis carnii*, a pulmonary fungal parasite that causes fatal pneumonia, at a low frequency (2.5%); other recorded lung parasites include the fungus *Chrysosporium* and protozoan *Hepatozoon* (Laakkonen et al. 2001).

A variety of ectoparasites occur on *M. californicus*, including lice, fleas (*Anomiopsyllus falsicalifornicus*, *Atyphloceras multidentatus*, *Catallagia wymani*, *Hystrichopsylla occidentalis linsdalei*, *Malaraeus telchinus*, *Nosopsyllus fasciatus*, and *Opisodasys keeni nesiotus*), ticks (*Dermacentor occidentalis* and *Ixodes angustus*), and mites (family Dermanyssidae, *Odontacarus hirsutus* and *Leeuwenhoekia americana*), including mange-causing scabies mites (*Notoedres muris*—Allred and Beck 1966; Barnes et al. 1977; Batzli and Pitelka 1971; Krasnov et al. 2004; Lidicker 1973; Nieto et al. 2007). Ectoparasite loads fluctuate by season and population density, peaking as populations decline (Lidicker 1973). Individual *M. californicus* can carry high loads of fleas and ticks (Nieto et al. 2007), and flea loads in nests are related to nest moisture content (Stark 2002). Ectoparasites can be removed in the field by ether anesthesia and vigorous brushing without affecting recapture success (VanBlankenstein and Botzler 1996). Fleas may be the primary source of plague infection, and flea removal eliminates seropositive animals in a population (Kartman and Hudson 1971).

Interspecific interactions.—*Microtus californicus* is often one of the most common members of the small mammal community (Johnston and Rudd 1957). In Mexico, *M. californicus* is part of the Northern Baja California region of endemism, often associated with the California pocket mouse (*Chaetodipus californicus*), San Diego pocket mouse (*C. fallax*), San Quintin kangaroo rat (*Dipodomys gravipes*), dusky-footed woodrat (*Neotoma fuscipes*), California deermouse (*Peromyscus californicus*), La Guarda deermouse (*P. guardia*), and Mearns's squirrel (*Tamiasciurus mearnsi*—Escalante et al. 2007). The North American deermouse (*Peromyscus maniculatus*) and western harvest mouse (*Reithrodontomys megalotis*) were commonly found in runways of *M. californicus* (Pearson 1960); however, *R. megalotis* avoided areas smelling of *M. californicus* both in the field and in the laboratory (Heske et al. 1984; Heske and Repp 1986). Avoidance was greatest when both species were reproductively active, although *M. californicus* showed no avoidance of *R. megalotis* (Heske and Repp 1986). *R. megalotis* also declines to very low numbers or becomes locally extirpated when density of *M. californicus* peaks during cyclic fluctuations (Heske et al. 1984). *M. californicus* moved less and instigated fewer approaches when placed in direct competition with *M. montanus* in an experimental arena and displayed mutual avoidance in 5 of 12 trials with other *Microtus* species (long-tailed vole [*M. longicaudus*], *M. montanus*, prairie vole [*M. ochrogaster*], and meadow vole [*M. pennsylvanicus*]—Colvin 1973a). *M. californicus* also is listed among the factors contributing to the extirpation of the house mouse (*Mus musculus*) on Brooks Island (Lidicker

1966). Mice began declining concurrently with the introduction and expansion of *M. californicus* on the island. Persistent annoyance of *M. musculus* by *M. californicus* may have contributed to a decreased reproductive rate and subsequent extirpation (Lidicker 1966).

Primary predators include hawks (American kestrel [*Falco sparverius*], northern harrier [*Circus cyaneus*], white-tailed kite [*Elanus leucurus*], and red-tailed hawk [*Buteo jamaicensis*]) and owls (barn owl [*Tyto alba*] and great horned owl [*Bubo virginianus*]), snakes (e.g., *Thamnophis*), mammalian predators such as weasels (long-tailed weasel [*Mustela frenata*] and ermine [*M. ermine*]), feral cat (*Felis catus*), gray fox (*Urocyon cinereoargenteus*), skunks (striped skunk [*Mephitis mephitis*] and western spotted skunk [*Spilogale gracilis*]), and coyote (*Canis latrans*), and wading birds such as herons and egrets (family Ardeidae—Heske and Lidicker 1999; Ingles 1965; Pearson 1960, 1964), and clapper rails (*Rallus longirostris levipes*), which are known to take *M. californicus* in salt marshes (Zedler 1982). Predators may negatively impact populations of *Microtus*, with mammalian predators removing up to 88% of a vole population in a given cycle (Pearson 1964). *Microtus* may represent the preferred food item and comprise the majority of a predator's diet; prey-switching at times of low vole densities may allow for predator persistence and continued predation pressure on vole populations (Pearson 1966, 1971).

Miscellaneous.—*Microtus californicus* can become an agricultural pest of vineyards and orchards, causing damage to bark and roots of orchard trees (Getz 1985). *M. californicus* is the most serious pest in artichoke fields; stomach contents of *M. californicus* collected from artichoke fields average 83.4% artichoke tissue (Koehler et al. 1989). Artichoke consumption was highest in winter (95.5%) and lowest in spring (59.1%), when an increased amount of native vegetation was consumed, perhaps as a result of reproductive nutritional requirements. Specialized feeding on artichokes may explain the inefficiency of rodenticide grain baits; rodenticide-treated artichoke bracts may serve as a more efficient pest treatment (Koehler et al. 1989). California voles have been found in other agricultural crops such as alfalfa, wheat, timothy (Getz 1985), potatoes (White 1965), and asparagus (Morrison 1953).

BEHAVIOR

Grouping behavior.—The social unit in *Microtus californicus* is the family group (Batzli 1968; Heske 1987b; Pearson 1960), typically composed of 1 male, 1 or more females, and their offspring (2–12 individuals—Pearson 1960). Both sexes can be territorial (Lidicker 1980), but females may form small aggregations; the bimodal pattern of intrasexual overlap among females suggests group defense of territories, although relationships of females within groups still need to be investigated (Heske 1987b; Ostfeld 1986). *M. californicus* is relatively tolerant of other individuals but displays increased aggression toward unknown voles (Hatfield 1935a). Males display higher levels of aggression, which may increase near estrous females (Ostfeld 1985), and males are highly aggressive to strange males, occasionally fatally wounding intruders (Heske 1987a). Aggression increases during the breeding season (Batzli and Pitelka 1971). Females display increased aggression while lactating and may fatally wound intruders (Lidicker 1966). Aggressive interactions include attacking with front claws or biting with incisors, the latter of which often results in severe injury (Hatfield 1935a). Wounds are most often inflicted on the flanks and tail, and voles often display missing digits (Ostfeld and Klosterman 1986). *M. californicus* produces clicking noises with its molars during aggressive encounters (Hatfield 1935a).

Rare instances of cannibalism were recorded in the laboratory and anecdotally from the field (Voge 1950). In one instance, part of the lungs, brain, and 1 eye were missing, the hind leg was skinned, and leg bones had been chewed; all or part of the intestines were missing in every instance (Voge 1950). Males are known to cannibalize unrelated neonates (Lidicker 1980).

Reproductive behavior.—*Microtus californicus* has been described as a "social moderate," midway between the "monogamous rigidity" and "rampant polygyny or promiscuity" observed for other vole species (Lidicker 1980). Monogamy may be more common at low densities with polygyny prominent at higher densities (Lidicker 1980), although no major shifts to pair formation were found when densities were reduced (Heske 1987b). When multiple individuals were placed in an enclosed area, wounding and subsequent mortality were initially high until voles were reduced to a single pair (Lidicker 1979). Alternatively, radiotelemetry and extensive trapping provide evidence for a polygynous mating system with female defense (Heske 1987b; Ostfeld 1986).

Males most commonly pursue females when attempting to mate; females will respond antagonistically to this pursuit when not in estrus (Hatfield 1935a). In rare instances, females may initiate mating. In 2 instances in the laboratory, the female began licking the ears and neck of the male while he rolled partially onto his back; both instances resulted in copulation (Hatfield 1935a).

Overall, *M. californicus* displayed more parental care than other species of congeners (Hartung and Dewsbury 1976). Both sexes often brood young in captivity (Hatfield 1935a), and males and females display no difference in parental care in captivity, as measured by time spent sitting on the nest, licking pups, manipulating nesting material, and pup retrieval (Hartung and Dewsbury 1976). Males spent significantly more time than females manipulating pups (Hartung and Dewsbury 1976); however, males become increasingly aggressive and may commit infanticide when young are about 1 month of age (Hatfield 1935a). Field observations suggest males are excluded from young in the wild (Hatfield 1935a), and radiotelemetry provided no evidence for paternal care (Ostfeld 1986). In the laboratory, females were more likely to display pregnancy interruption if the original male was replaced with a stranger; introduced males committed infanticide in 3 of 40 replacements (Heske 1987a).

Communication.—Young *Microtus californicus* produce ultrasound vocalizations to attract parental attention when placed in stressful situations; stress due to cold may be the primary factor eliciting ultrasonic calls (Colvin 1973b). Pups were effective at drawing parents to the nest when calling; males and females responded equally to calls of pups. Ultrasound production and pattern begin to deteriorate as neonates mature past 10 days, concurrent with the time pups become more independent and rely less on mothers (Colvin 1973b). Females do not appear to chase weaned juveniles from the nest (Pearson 1960).

Only male *M. californicus* have hip glands, which appear associated with reproduction, although exact function is unknown (Lidicker 1980). Males scent-mark sides of plastic tubes simulating runway conditions; females may also scent-mark, despite lacking hip glands. Hip glands may be targeted in aggressive encounters and are often sites of wounding (Lidicker 1980).

Miscellaneous behavior.—*Microtus californicus* remains active year-round and does not hibernate (Lidicker 1973). Although *M. californicus* may be active throughout the day, majority of activity occurs around dawn and dusk, with voles becoming more nocturnal during hot and dry summer days (Heske and Lidicker 1999). Hatfield (1935a) found *M. californicus* more active during the night in the laboratory and field. Peaks of activity were observed in low-intensity light, when voles were exposed both to darkness and light simulating 15% starlight (Kavanau and Havenhill 1976). *M. californicus* demonstrates increased runway activity on moonless nights and during rainy periods of the wet winter (Pearson 1960).

Young *M. californicus* display depth perception by weaning; individuals demonstrated a significant preference for the shallow side of a visual cliff (Sloane et al. 1978). Adults have a 270-degree field of vision vertically and horizontally and length of sight between 3.05 and 3.66 m (Hatfield 1935a). Auditory cues made by rustling grass produce an immediate reaction, probably due to similarity of the sound of rustling grass made by predators (Hatfield 1935a). Foraging behavior includes standing on hind legs and clipping grass stems to gain access to seed heads (Heske and Lidicker 1999). *M. californicus* brings food back to burrows (grass blades and stems and herb leaves—Pearson 1960); however, *M. californicus* does not exhibit food caching behavior (Lidicker 1980; but see Batzli and Pitelka [1971] for potential caching of seeds). *M. californicus* is a strong swimmer and may dive and remain underwater with only the nose protruding to escape from predators, although no voles displaying this antipredator behavior were successful (Johnston 1957). Dives were usually <10 s and could cover up to 3.05 m (Johnston 1957). Other nonsocial behaviors include locomotive and exploratory movements, grooming, freezing, and rearing at walls; *M. californicus* is not known to climb walls (Hooper and Hart 1962).

GENETICS

Cytogenetics.—*Microtus californicus* has karyotypic variation (Gill 1982). Diploid number (2n) is polymorphic, with 52, 53, or 54 chromosomes (Gill 1982). Chromosomes are medium in size, but display variation (Mathey 1954). The Y chromosome is short; the X chromosome is V-shaped with subequal arms. Most chromosomes are acrocentric (Mathey 1954), but the metacentric X chromosome, 3 large submetacentrics (usually including the largest chromosome pair), and 2 small metacentrics are found in almost all karyotypes of *M. c. californicus*, *M. c. stephensi*, and *M. c. sanctidiegi*, with an additional rare large metacentric (Gill 1982). The 2nd largest acrocentric may have a maximum of 3 G-banded variants and is often unpaired. The short arm of the largest submetacentric may demonstrate an inversion (Gill 1982).

Molecular genetics.—Coat color is determined by a single polymorphic locus, with an agouti dominant wild type and a buffy recessive homozygote (Lidicker 1963). In laboratory breeding experiments, heterozygotic individuals display higher reproductive fitness (Gill 1977b). The polymorphism may be maintained by a trade-off between lower reproductive success of homozygotes and potentially greater predation pressure on buffy individuals, which is somewhat supported by a fairly high frequency of buffy recessives in an island population subjected to fewer predator species than mainland populations (Gill 1977b).

Population genetics.—An introduced population on Brooks Island, California, demonstrated an increased incidence of white spotting on the chin (Gill 1976). Spots ranged in size and length of extension down the throat; spot size tended to increase when both parents were spotted. Spotting was associated with homozygous agouti individuals; presence of a buffy allele reduced the incidence of spotting. Spotted females produced fewer young, although presence of spotting was more important to reproductive fitness than was spot size. Mode of inheritance is unknown (Gill 1976). Other reported coat-color polymorphisms include white body with brown hair on ears and sides of backbone and a dark gray pelvic area, collected 10 miles southwest of Gridley, Butte County, California (Fisher 1942); a white-spotted agouti collected from Fort Tejon, California (Owen and Shakelford 1942); and 3 yellow morphs from Concord, Contra Costa County, California (Orr 1941). The yellow specimens displayed pink dorsal pelage in the female and buff pelage in the male distally, dorsal light-gray pelage proximally, creamy white tails, cream-colored vibrissae, and unpigmented tail, claws, and foot pads. Color variation may result from a change in the factor controlling melanin production in fur and skin (Orr 1941).

Microtus californicus is distributed nearly continuously during population peaks and in isolated populations during population crashes. Bowen (1982) examined changes in 4 polymorphic loci of a natural population of *M. californicus* spanning 2 periods of low density and a population peak. As expected, the most common allele increased following a population bottleneck, and, in some cases, became fixed; however, many rare alleles lost in the study population were found to persist in other populations. F_{ST} values were lowest and heterogeneity highest during population peaks, indicating lower levels of differentiation and greater genetic connectedness during periods of high density, perhaps as a result of increased dispersal at the onset of breeding season (Bowen 1982).

Microtus californicus may be most closely related to the Mexican vole (*M. mexicanus*), both of which may derive from a lineage including *M. montanus* and *M. townsendii* (Anderson 1959). A successful laboratory mating of a female *M. californicus* and male *M. montanus* resulted in 4 young, only 1 of which survived to at least 9 months; reproductive fate is unknown (Hatfield 1935a). Attempts to hybridize *M. c. californicus* and *M. c. stephensi* had little success (Gill 1980). All hybrid males were sterile due to an inability to produce sperm; hybrid females demonstrated reduced fertility when backcrossed to nonhybrid males. Although genetic distance between subspecies was similar to that observed for other mammalian subspecies, a variety of genetic and morphological characteristics (including skull length and heart mass) can be used to distinguish between these subspecies. The relatively low hybridization success observed may demonstrate 2 subspecies currently diverging to species status; however, the geographically intermediate subspecies, *M. c. sanctidiegi*, was not included in analysis (Gill 1980). Molecular data further support distinct northern and southern clades with limited gene flow at the contact zone in Santa Barbara, Kern, and Ventura counties, California (Conroy and Neuwald 2008). The phylogeographic break does not appear to follow subspecies boundaries, and the 4.46% average genetic distance between clades may warrant splitting into 2 distinct species (Conroy and Neuwald 2008).

CONSERVATION

Habitat suitable for *Microtus californicus* has been drastically altered and reduced by human activities, such as wetland draining for agriculture and filling of salt marshes for industrial purposes (Getz 1985). *M. californicus* was presumed to inhabit large, contiguous, and relatively stable habitats prior to human alteration but now may be restricted to ungrazed and less-disturbed grasslands, potentially containing a large number of exotic plant species (Getz 1985). Contaminants in salt-marsh habitats surrounding San Francisco Bay (including mercury, selenium, cadmium, and lead) may further jeopardize populations of *M. californicus* (Clark et al. 1992). Although captured individuals carried trace amounts of each contaminant, individuals appeared relatively healthy and able to tolerate current contaminant levels, which were below maximum levels recorded elsewhere for other mice and vole populations (Clark et al. 1992).

Microtus californicus is listed as a species of “Least Concern” on the International Union for Conservation of Nature and Natural Resources (2010) *Red list of threatened species*, although several subspecies are listed for protection or recognized as imperiled. The California Department of Fish and Game (2008) recognizes *M. c. halophilus* as a critically imperiled subspecies with a greatly restricted range in which it can be locally common, and *M. c. sanpabloensis*, *M. c. stephensi*, *M. c. vallicola*, and *M. c. mohavensis* as subspecies of special concern in large part due to habitat loss and the isolated nature of populations (Williams 1986); *M. c. vallicola* also is listed as sensitive by the California Bureau of Land Management (2006). *M. c. mohavensis* is likely threatened by anthropogenic development of land, although additional habitat may be provided by irrigated pasture and alfalfa fields (Williams 1986). *M. c. grinnelli* and *M. c. huperuthrus* are believed to be extinct (Heske and Lidicker 1999), and the entire species (including *M. c. grinnelli*, *M. c. huperuthrus*, and *M. c. aequivocatus*) may be extirpated from Baja California due to habitat destruction (Ceballos and Navarro 1991).

Microtus californicus scirpensis has been cited as extinct as recently as 1976, presumably due to habitat loss (Nowak 1976); however, the subspecies was “rediscovered” within the next 3 years with the capture of 21 individuals (Bleich 1979). *M. c. scirpensis* is currently offered protection as an endangered subspecies under both the United States (United States Fish and Wildlife Service 1997, 2008) and California (California Department of Fish and Game 2008; Williams 1986) Endangered Species acts as well as listed as vulnerable by the International Union for Conservation of Nature and Natural Resources (2010). This subspecies has an extremely limited and disjunct distribution in the central Mojave Desert and is restricted to isolated wetland habitats and springs along the Amargosa River. Major threats include wetland conversion for farming, diversion of surface and groundwater, intermittent flooding, and nonnative species (United States Fish and Wildlife Service 1997). The development of an Area of Critical Environmental Concern has since reduced burning and cattle grazing in federally owned habitat of *M. c. scirpensis*; however, diversion of groundwater, encroachment by salt cedar (*Tamarix*), predation by feral cats, potential competitive interactions with *Mus musculus*, and low genetic diversity may still pose major threats (United States Fish and Wildlife Service 2009).

ACKNOWLEDGMENTS

W. Lidicker generously provided a photograph of a live animal, and M. Bucci, C. Cudworth, and R. Minor assisted in photographing the skull. The distribution map was created by M. Merrick. E. Heske and 1 anonymous reviewer provided helpful comments on earlier drafts.

LITERATURE CITED

Allred, D. M. 1952. Plague important fleas and mammals in Utah and the western United States. Great Basin Naturalist 12:67–71.

Allred, D. M., and D. E. Beck. 1966. Mites of Utah mammals. Brigham Young University Science Bulletin 8:1–123.

Anderson, S. 1959. Distribution, variation, and relationships of the montane vole, *Microtus montanus*. University of Kansas Publications, Museum of Natural History 9:415–511.

Anderson, S. 1960. The baculum in microtine rodents. University of Kansas Publications, Museum of Natural History 12:181–216.

Bailey, V. 1898. Descriptions of eleven new species and subspecies of voles. Proceedings of the Biological Society of Washington 12: 85–90.

Bailey, V. 1900. Revision of American voles of the genus *Microtus*. North American Fauna 17:1–88.

Baird, S. F. 1857. Mammals of North America; the descriptions of species based chiefly on the collections in the Museum of the Smithsonian Institution. J. B. Lippincott & Co., Philadelphia, Pennsylvania.

Barnes, A. M., V. P. Tipton, and J. A. Wildie. 1977. The subfamily Anomiopsyllinae (Hystrichopsyllidae: Siphonaptera). 1. A revision of the genus *Anomiopsyllus* Baker. Great Basin Naturalist 37: 138–206.

Batzli, G. O. 1968. Dispersion patterns of mice in California annual grassland. Journal of Mammalogy 49:239–250.

Batzli, G. O. 1974. Influence of habitat structure on a population of voles. Bulletin of the Southern California Academy of Science 73: 83–85.

Batzli, G. O., and F. R. Cole. 1979. Nutritional ecology of microtine rodents: digestibility of forage. Journal of Mammalogy 60: 740–750.

Batzli, G. O., L. L. Getz, and S. S. Hurley. 1977. Suppression of growth and reproduction of Microtine rodents by social factors. Journal of Mammalogy 58:583–591.

Batzli, G. O., and F. A. Pitelka. 1971. Condition and diet of cycling populations of the California vole, *Microtus californicus*. Journal of Mammalogy 52:141–163.

Batzli, G. O., R. G. White, S. F. MacLean, Jr., F. A. Pitelka, and B. D. Collier. 1980. The herbivore-based trophic system. Pp. 335–410 in An Arctic ecosystem: the coastal tundra at Barrow, Alaska (J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell, eds.). Dowdon, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

Bell, C. J., and G. S. Bever. 2006. Description and significance of the *Microtus* (Rodentia: Arvicolinae) from the type Irvington fauna, Alameda County, California. Journal of Vertebrate Paleontology 26:371–380.

Bennett, S. G., et al. 1999. *Hantavirus* (*Bunyaviridae*) infections in rodents from Orange and San Diego counties, California. American Journal of Tropical Medicine and Hygiene 60:75–84.

Bleich, V. C. 1979. *Microtus californicus scirpensis* not extinct. Journal of Mammalogy 60:851–852.

Bowen, B. S. 1982. Temporal dynamics of microgeographic structure of genetic variation in *Microtus californicus*. Journal of Mammalogy 63:625–638.

Bradley, S. R. 1976. Temperature regulation and bioenergetics of some microtine rodents. Ph.D. dissertation, Cornell University, Ithaca, New York.

California Bureau of Land Management. 2006. California—BLM animal sensitive species list. Updated September 2006. www.blm.gov/ca/pdfs/pa_pdfs/biology_pdfs/SensitiveAnimals.pdf, accessed 22 April 2008.

California Department of Fish and Game. 2008. Special animals. Updated February 2008. www.dfg.ca.gov/biogeodata/cnddb/plants_and_animals.asp, accessed 22 April 2008.

Carleton, M. D. 1985. Macroanatomy. Pp. 116–175 in Biology of New World *Microtus* (R. H. Tamarin, ed.), Special Publication 8, The American Society of Mammalogists.

Ceballos, G., and D. Navarro L. 1991. Diversity and conservation of Mexican mammals. Pp. 167–198 in Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman.

Church, R. L. 1966. Water exchanges of the California vole, *Microtus californicus*. Physiological Zoology 39:326–340.

Clark, D. R., Jr., K. S. Forester, C. M. Marn, and R. L. Hothem. 1992. Uptake of environmental contaminants by small mammals in pickleweed habitats at San Francisco Bay, California. Archives of Environmental Contamination and Toxicology 22:389–396.

Clements, F. E. 1936. The origin of the desert climax and climate. Pp. 87–140 in Essays in geobotany in honor of William Allen Setchell (T. H. Goodspeed, ed.). University of California Press, Berkeley.

Colvin, D. V. 1973a. Agnostic behaviour in males of five species of voles *Microtus*. Animal Behavior 21:471–480.

Colvin, M. A. 1973b. Analysis of acoustic structure and function in ultrasounds of neonatal *Microtus*. Behaviour 44:234–263.

Colvin, M. A., and D. V. Colvin. 1970. Breeding and fecundity of six species of voles (*Microtus*). Journal of Mammalogy 51:417–419.

Conroy, C. J., and J. L. Neuwald. 2008. Phylogeographic study of the California vole, *Microtus californicus*. Journal of Mammalogy 89: 755–767.

Ecke, D. H., and A. R. Kinney. 1956. Aging meadow mice, *Microtus californicus*, by observation of molt progression. Journal of Mammalogy 37:249–254.

Elliot, D. G. 1903. Description of apparently new species and subspecies of mammals from California, Oregon, the Kenai Peninsula, Alaska, and Lower California, Mexico. Field Columbian Museum Publications, Zoology Series 3:153–173.

Escalante, T., V. Sanchez-Cordero, J. J. Morrone, and M. Linaje. 2007. Areas of endemism of Mexican terrestrial mammals: a case study using species' ecological niche modeling, parsimony analysis of endemicity, and Goloboff fit. Interciencia 32:151–159.

Fisher, H. I. 1942. A white meadow mouse. Journal of Mammalogy 23: 336.

Ford, R. G., and F. A. Pitelka. 1984. Resource limitation in populations of the California vole. Ecology 65:122–136.

Gardner, L. L. 1917. A partial list of mammals of the Claremont region. Journal of Entomology and Zoology 9:101–106.

Garsd, A., and W. E. Howard. 1981. A 19-year study of microtine population fluctuations using time-series analysis. Ecology 62: 930–937.

Getz, L. L. 1985. Habitats. Pp. 286–309 in Biology of New World *Microtus* (R. H. Tamarin, ed.), Special Publication 8, The American Society of Mammalogists, Lawrence, Kansas.

Gill, A. E. 1976. White spotting in the California vole. Heredity 37: 113–128.

Gill, A. E. 1977a. Food preferences of the California vole, *Microtus californicus*. Journal of Mammalogy 58:229–233.

Gill, A. E. 1977b. Maintenance of polymorphism in an island population of the California vole, *Microtus californicus*. Evolution 31:512–525.

Gill, A. E. 1980. Partial reproductive isolation of the California vole, *Microtus californicus*. Genetica 52/53:105–117.

Gill, A. E. 1982. Variability in the karyotype of the California vole, *Microtus californicus*. Mammalian Chromosomes Newsletter 23: 18.

Gill, A. E., and K. Bolles. 1982. A heritable tooth trait varying in two subspecies of *Microtus californicus* (Rodentia: Cricetidae). Journal of Mammalogy 63:96–103.

Greenwald, G. S. 1956. The reproductive cycle of the field mouse, *Microtus californicus*. Journal of Mammalogy 37:213–222.

Greenwald, G. S. 1957. Reproduction in a coastal California population of the field mouse, *Microtus californicus*. University of California Publications in Zoology 57:421–446.

Grinnell, J. 1926. Critical examination of the meadow mice of Lower California. Journal of Mammalogy 7:221–226.

Hall, E. R. 1981. The mammals of North America. 2nd ed. John Wiley & Sons, Inc., New York.

Hartung, T. G., and D. A. Dewsbury. 1976. Parental behavior in six species of muroid rodents. Behavioral and Neural Biology 26: 466–478.

Hatfield, D. M. 1935a. A natural history study of *Microtus californicus*. Journal of Mammalogy 16:261–271.

Hatfield, D. M. 1935b. Description of a new race of *Microtus californicus*. Journal of Mammalogy 16:316–318.

Heske, E. J. 1987a. Pregnancy interruption by strange males in the California vole. Journal of Mammalogy 68:406–410.

Heske, E. J. 1987b. Spatial structuring and dispersal in a high density population of the California vole *Microtus californicus*. Holarctic Ecology 10:137–148.

Heske, E. J., and W. Z. Lidicker, Jr. 1999. California vole: *Microtus californicus*. Pp. 626–628 in The Smithsonian book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution Press, Washington, D.C.

Heske, E. J., and R. S. Ostfeld. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. Journal of Mammalogy 71:510–519.

Heske, E. J., R. S. Ostfeld, and W. Z. Lidicker, Jr. 1984. Competitive interactions between *Microtus californicus* and *Reithrodontomys megalotis* during two peaks of *Microtus* abundance. Journal of Mammalogy 65:271–280.

Heske, E. J., and R. M. Repp. 1986. Laboratory and field evidence for the avoidance of California voles (*Microtus californicus*) by western harvest mice (*Reithrodontomys megalotis*). Canadian Journal of Zoology 64:1530–1534.

Hilborn, R. 1974. Inheritance of skeletal polymorphism in *Microtus californicus*. Heredity 33:87–89.

Hoffmann, R. S. 1958. The role of reproduction and mortality in population fluctuations of voles (*Microtus*). Ecological Monographs 28:79–109.

Hoffmann, R. S., and J. W. Koeppl. 1985. Zoogeography. Pp. 84–115 in Biology of New World *Microtus* (R. H. Tamarin, ed.), Special Publication 8, The American Society of Mammalogists.

Hooper, E. T., and B. S. Hart. 1962. A synopsis of recent North American microtine rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan 120:1–68.

Houlihan, R. T. 1963. The relationship of population density to endocrine and metabolic changes in the California vole, *Microtus californicus*. University of California Publications in Zoology 65: 327–362.

Huey, L. M. 1931. A new meadow mouse from Lower California, Mexico. Transactions of the San Diego Society of Natural History 7:47–50.

Huey, L. M. 1964. The mammals of Baja California, Mexico. Transactions of the San Diego Society of Natural History 13: 85–168.

Ingles, L. G. 1965. Mammals of the Pacific states. Stanford University Press, Palo Alto, California.

International Union for Conservation of Nature and Natural Resources. 2010. 2010 International Union for Conservation of Nature and Natural Resources Red list of threatened species. www.iucnredlist.org, accessed 10 September 2010.

Jameson, E. W., Jr. 1958. Consumption of alfalfa and wild oats by *Microtus californicus*. The Journal of Wildlife Management 22: 433–435.

Johnston, R. F. 1957. Adaptation of salt marsh mammals to high tides. Journal of Mammalogy 38:529–531.

Johnston, R. F., and R. L. Rudd. 1957. Breeding of the salt marsh shrew. Journal of Mammalogy 38:157–163.

Kartman, L., and B. W. Hudson. 1971. The effect of flea control on *Yersinia* (*Pasteurella*) *pestis* antibody rates in the California vole, *Microtus californicus*, and its epizootiological implications. Bulletin of the World Health Organization 45:295–301.

Kartman, L., S. F. Quan, and H. E. Stark. 1962. Ecological studies of wild rodent plague in the San Francisco Bay area of California. VII. Effects of plague in nature on *Microtus californicus* and other wild rodents. Zoonoses Research 1:99–119.

Kavanau, J. L., and R. M. Havenhill. 1976. Compulsatory regime and control of environment in animal behavior. III Light level preferences of small nocturnal mammals. Behaviour 59:203–225.

Kellogg, R. 1918. A revision of the *Microtus californicus* group of meadow mice. University of California Publications in Zoology 21:1–42.

Kellogg, R. 1922. Change of name. Proceedings of the Biological Society of Washington 35:78.

Kenagy, G. J., and O. P. Pearson. 2000. Life with fur and without: experimental field energetics and survival of naked meadow voles. Oecologia 122:220–224.

Kenney, A. M., T. G. Hartung, and D. A. Dewsbury. 1979. Copulatory behavior and the initiation of pregnancy in California voles (*Microtus californicus*). Brain Behavior and Evolution 16: 176–191.

Koehler, A. E., R. E. Marsh, A. D. Tunberg, and W. E. Howard. 1989. Food habits of California voles, *Microtus californicus*, in artichokes, *Cynara scolymus*. Crop Protection 8:114–117.

Krasnov, B. R., I. S. Khokhlova, and G. I. Shenbrot. 2004. Sampling fleas: the reliability of host infestation data. Medical and Veterinary Entomology 18:232–240.

Krebs, C. J. 1966. Demographic changes in fluctuation populations of *Microtus californicus*. Ecological Monographs 36:239–273.

Krohne, D. T. 1980. Intraspecific litter size variation in *Microtus californicus* II: variation between populations. Evolution 34: 1174–1182.

Krohne, D. T. 1981. Intraspecific litter size variation in *Microtus californicus*: variation within populations. Journal of Mammalogy 62:29–40.

Krohne, D. T. 1982. The demography of low-litter size populations of *Microtus californicus*. Canadian Journal of Zoology 60:368–374.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Laakkonen, J., R. N. Fisher, and T. J. Case. 2001. Pneumocystosis in wild small mammals from California. Journal of Wildlife Diseases 37:408–412.

Le Conte, J. 1853. Description of three new species of American *Arvicola*, with remarks upon some other American rodents. Proceedings of the Academy of Natural Sciences of Philadelphia 6:404–415.

Lidicker, W. Z., Jr. 1963. The genetics of a naturally occurring coat-color mutation in the California vole. Evolution 17:340–346.

Lidicker, W. Z., Jr. 1966. Ecological observations on a feral house mouse population declining to extinction. Ecological Monographs 36:27–50.

Lidicker, W. Z., Jr. 1973. Regulation of numbers in an island population of California vole, a problem in community dynamics. Ecological Monographs 43:271–302.

Lidicker, W. Z., Jr. 1976. Experimental manipulation of the timing of reproduction in the California vole. Researches on Population Ecology 18:14–27.

Lidicker, W. Z., Jr. 1979. Analysis of two freely-growing enclosed populations of the California vole. Journal of Mammalogy 60: 447–466.

Lidicker, W. Z., Jr. 1980. The social biology of the California vole. Biologist 62:46–55.

Lidicker, W. Z., Jr., and P. K. Anderson. 1962. Colonization of an island by *Microtus californicus*, analyzed on the basis of runway transects. Journal of Animal Ecology 31:503–517.

Lidicker, W. Z., Jr., and R. S. Ostfeld. 1991. Extra-large body size in California voles: causes and fitness consequences. Oikos 61: 108–121.

Mathey, R. 1954. Nouvelles reserches sur les chromosomes des Muridae. Caryologica 6:1–44.

Morrison, A. E. 1953. The meadow mouse (*Microtus californicus*) problem in Sacramento County. California Department of Agriculture Bulletin 42:59–62.

Mullen, D. A. 1960. Adrenal weight changes in *Microtus*. Journal of Mammalogy 41:129–130.

Musser, G. G., and M. D. Carleton. 2005. Superfamily Muroidea. Pp. 894–1531 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.), 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

Nelson, R. J., J. Dark, and I. Zucker. 1983. Influence of photoperiod, nutrition and water availability on reproduction of male

California voles (*Microtus californicus*). Journal of Reproduction and Fertility 69:473–477.

Nieto, N. C., et al. 2007. Ectoparasite diversity and exposure to vector-borne disease agents in wild rodents in central coastal California. Journal of Medical Entomology 44:328–335.

Nowak, R. M. 1976. Our American wildlife: 1776–1976. National Parks and Conservation Magazine: The Environmental Journal 50:14–18.

Orr, R. T. 1941. Yellow mutation in the California meadow mouse, *Microtus californicus* (Peale). Wasmann Collector 4:129–130.

Osgood, W. H. 1928. Why is a type specimen. Journal of Mammalogy 9:52–56.

Ostfeld, R. S. 1985. Experimental analysis of aggression and spacing behavior in California voles. Canadian Journal of Zoology 63: 2277–2282.

Ostfeld, R. S. 1986. Territoriality and mating system of California voles. Journal of Animal Ecology 55:691–706.

Ostfeld, R. S., and L. L. Klosterman. 1986. Demographic substructure in a California vole population inhabiting a patchy environment. Journal of Mammalogy 67:693–704.

Ostfeld, R. S., W. Z. Lidicker, Jr., and E. J. Heske. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. Oikos 45: 433–442.

Owen, R. D., and R. M. Shackelford. 1942. Aberrations in *Microtus* and *Pitymys*. Journal of Mammalogy 23:306–314.

Peale, T. R. 1848. Mammalia and ornithology. Reprint edition 1978. Arno Press Inc., New York.

Pearson, O. P. 1960. Habits of *Microtus californicus* revealed by automatic photographic recorders. Ecological Monographs 30: 232–250.

Pearson, O. P. 1964. Carnivore–mouse predation: an example of its intensity and bioenergetics. Journal of Mammalogy 45:177–188.

Pearson, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. Journal of Animal Ecology 35:217–233.

Pearson, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). Journal of Mammalogy 52:41–49.

Peavey, C. A., R. S. Lane, and J. E. Kleinjan. 1997. Role of small mammals in the ecology of *Borrelia burgdorferi* in a peri-urban park in north coast California. Experimental and Applied Acarology 21:569–584.

Quan, S. F., and L. Kartman. 1962. Ecological studies of wild rodent plague in the San Francisco Bay area of California. VIII. Susceptibility of wild rodents to experimental plague infection. Zoonoses Research 1:121–144.

Quay, W. B. 1954a. The meibomian glands of voles and lemmings (Microtinae). Miscellaneous Publications of the Museum of Zoology, University of Michigan 82:1–23.

Quay, W. B. 1954b. The anatomy of the diastemal palate in microtine rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan 86:1–49.

Regnery, D. C. 1987. Isolation and partial characterization of an orthopoxvirus from a California vole (*Microtus californicus*). Archives of Virology 94:159–162.

Repenning, C. A. 1980. Faunal exchanges between Siberia and North America. Canadian Journal of Anthropology 1:37–44.

Repenning, C. A. 1987. Biochronology of the microtine rodents of the United States. Pp. 236–268 in Cenozoic mammals of North America (M. O. Woodburne, ed.). University of California Press, Berkeley.

Repenning, C. A. 1992. *Allophaiomys* and the age of the Olyor Suite, Krestovka Sections, Yakutia. United States Geological Survey Bulletin 2037:1–98.

Rissman, E. F., and R. E. Johnston. 1985. Female reproductive development is not activated by male California voles exposed to family cues. Biology of Reproduction 32:352–360.

Selle, R. M. 1928. *Microtus californicus* in captivity. Journal of Mammalogy 9:93–98.

Sloane, S. A., S. L. Shea, M. M. Proctor, and D. A. Dewsbury. 1978. Visual cliff performance in 10 species of muroid rodents. Animal Learning and Behavior 6:244–248.

Song, W. M., et al. 1995. Isla Vista virus: a genetically novel hantavirus of the California vole *Microtus californicus*. Journal of General Virology 76:3195–3199.

Stark, H. E. 1963. Nesting habits of the California vole, *Microtus californicus*, and microclimate factors affecting its nests. Ecology 44:663–669.

Stark, H. E. 2002. Population dynamics of adult fleas (Siphonaptera) on hosts and in nests of the California voles. Journal of Medical Entomology 39:818–824.

Thaeler, C. S., Jr. 1961. Variation in some salt-marsh populations of *Microtus californicus*. University of California Publications in Zoology 60:67–94.

Trouessart, E. L. 1897. Catalogus mammalium tam viventium quam fossilium. Fasciculus III. Rodentia II. Myomorpha, Hystrichomorpha, Lagomorpha. R. Friedländer and Sohn, Berlin, Germany.

United States Fish and Wildlife Service. 1997. Amargosa vole (*Microtus californicus scirpensis*) recovery plan. United States Fish and Wildlife Service, Portland, Oregon.

United States Fish and Wildlife Service. 2008. Endangered species program. www.fws.gov/endangered/wildlife.html, accessed 22 April 2008.

United States Fish and Wildlife Service. 2009. Amargosa vole (*Microtus californicus scirpensis*) 5-year review: summary and evaluation. United States Fish and Wildlife Service, Ventura, California.

Vanblankenstein, T., and R. G. Botzler. 1996. Effect of ectoparasite removal procedures on recapture of *Microtus californicus*. Journal of Wildlife Diseases 32:714–715.

Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley.

Voge, M. 1950. Cannibalism in *Microtus californicus*. Journal of Mammalogy 31:96.

Voge, M., and H. A. Bern. 1949. Cecal villi in the red tree mouse, *Phenacomys longicaudus*. Anatomical Records 104:477–482.

Von Bloeker, J. C., Jr. 1932. Three new mammals from salt marsh areas in southern California. Proceedings of the Biological Society of Washington 45:131–138.

Von Bloeker, J. C., Jr. 1937. Four new rodents from Monterey County, California. Proceedings of the Biological Society of Washington 50:153–158.

Vredevoe, L. K., J. R. Stevens, and B. S. Schneider. 2004. Detection and characterization of *Borrelia bissettii* in rodents from the central California coast. Journal of Medical Entomology 31: 736–745.

White, L. 1965. Biological and ecological considerations in meadow mouse population management. California Department of Agriculture Bulletin 54:161–167.

Williams, D. F. 1986. Mammalian species of special concern in California. California Department of Fish and Game, Wildlife Management Division Administrative Report 86-1:1–100.

Zagorodnyuk, I. V. 1990. Kariotipicheskaya izmenchivost' i sistematika serykh polevok (Rodentia, Arvicolini). Soobshchenie 1. Vidovoi sostav i khromosomnye chisla [Karyotypic variability and systematics of the gray voles (Rodentia, Arvicolini). Communication 1. Species composition and chromosomal number.] Vestnik Zoologii 2:26–37 (in Russian).

Zakrzewski, R. J. 1972. Fossil microtines from late Cenozoic deposits in the Anza-Borrego Desert, California, with the description of a new subgenus of *Synaptomys*. Natural History Museum of Los Angeles County. Contributions in Science 221:1–12.

Zakrzewski, R. J. 1985. The fossil record. Pp. 1–51 in Biology of New World *Microtus* (R. H. Tamarin, ed.), Special Publication 8, The American Society of Mammalogists.

Zedler, J. B. 1982. The ecology of southern California coastal salt marshes: a community profile. FWS/OBS-81/54. United States Fish and Wildlife Service Biological Services Program, Washington, D.C.

Ziegler, A. C. 1961. Occurrence of os clitoridis in *Microtus*. Journal of Mammalogy 42:101–103.

Associate editor of this account was Eric Rickart. Ryan Norris reviewed the synonymy. Editor was Meredith J. Hamilton.