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## Clethrionomys californicus.

By Lois F. Alexander and B. J. Verts

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## Clethrionomys californicus (Merriam, 1890)

Western Red-backed Vole

Evotomys californicus Merriam, 1890:26. Type locality "Eureka, Humboldt County, California."

Evotomys mazama (Merriam, 1897:71). Type locality "Crater Lake, south end of Cascade Range, Oregon."

Evotomys obscurus (Merriam, 1897:72). Type locality "Prospect, Upper Rogue River Valley, Oregon (at west base of Mount Mazama, altitude about 2600 feet or 800 meters)."

Clethrionomys californicus: Bailey, 1936:191. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Arvicolinae, Genus *Clethrionomys* (Carleton and Musser, 1984). Three subspecies are recognized currently (Hall, 1981):

C. c. californicus (Merriam, 1890:26), see above.

C. c. mazama (Merriam, 1897:71), see above.

C. c. obscurus (Merriam, 1897:72), see above.

Only two subspecies, C. c. californicus and C. c. mazama, were recognized by Maser and Maser (1988); however, they did not explain their view.

DIAGNOSIS. Clethrionomys californicus (Fig. 1) has a chestnut brown to reddish brown dorsal stripe grading to dark gray or buffy gray on the sides and belly; the tail is long and indistinctly bicolored, dusky above and whitish below (Bailey, 1936; Ingles, 1965; Merriam, 1890). Juveniles are darker and have a less distinct median stripe on the dorsum (Bailey, 1936; Maser and Storm, 1970; Maser et al., 1981). C. c. californicus is darker than the other two subspecies with the red on the back "much obscured or sometimes wholly concealed by black"; C. c. mazama is lighter colored and C. c. obscurus is intermediate (Bailey, 1936:191). The pelage is long and soft in winter and short and coarse in summer.

Clethrionomys californicus can be distinguished from sympatric vole-like mammals as follows: from Phenacomys (including Arborimus) by M3 possessing four loops of enamel on the lingual side and reentrant angles on lower molars not exceeding half the width of the teeth; from Microtus by molars rooted in adults and most loops of enamel on upper molars rounded; and from  $M.\ oregoni$ (of similar size) by an eye >4 mm in diameter, four loops of enamel on lingual side of M3, and molars rooted in adults (Hall, 1981; Hall and Cockrum, 1953; Ingles, 1965; Verts and Carraway, 1984). C. californicus is distinguished from C. gapperi by posterior margin of palate with a thin triangular shelf (median spine-Bee and Hall, 1956; Maser and Storm, 1970; Verts and Carraway, 1984) and indistinct reddish stripe on dorsum (Hall and Cockrum, 1953); and from C. rutilus by postpalatal bridge complete even in half-grown young, pretympanic fenestra <20% of a circle, tail slender, and hairs on tail short except on tip (Hall, 1981; Hall and Cockrum,

GENERAL CHARACTERISTICS. Ranges in external measurements (in mm) of *C. californicus* are: total length, 121–165; length of tail, 34–56; length of hind foot, 17–21; length of ear, 10–14 (Bailey, 1936; Hall, 1981; Hall and Cockrum, 1953; Ingles, 1965; Jameson and Peeters, 1988; Maser and Storm, 1970; Merriam, 1890; Stephens, 1906). Body mass of adults ranges from 15 to 40 g (Maser et al., 1981; Nowak and Paradiso, 1983). Ranges of selected skull measurements (in mm) of six specimens of *C. californicus* are: basal length, 21.8–23.3; zygomatic breadth, 13.3–44.2; mastoid breadth, 11.5–12.4; length of nasals, 7.2–7.5; and "upper molars, alveolar," 4.5–5.3 (Hinton, 1926:441). Mean width of the first loop of the third upper molar in *C. californicus* is 0.89 mm (range, 0.75–1.05; n = 21—Sheppe, 1960).

The auditory bullae are large and the pterygoid processes are relatively heavy (Fig. 2). The dentition is characterized by relatively wide and heavy cheek teeth; M3 and m1 have a simplified enamel pattern, with a reduced number of salient and reentrant angles (Hall and Cockrum, 1953; Hinton, 1926; Orr, 1945). The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

DISTRIBUTION. The geographic range of *C. californicus* (Fig. 3) includes western Oregon and northern California, from the Columbia River south to ca. 100 km N San Francisco Bay, California. *C. californicus* ranges from the Pacific Ocean (MacNab and Dirks, 1941) to the summit of the Cascade Range (Hinton, 1926; MacNab and Dirks, 1941; Stephens, 1906) and occupies Transition and Canadian life zones (Bailey, 1936). There is no fossil record for *C. californicus* (E. Anderson, pers. comm.).

FORM AND FUNCTION. The baculum of *C. californicus* (Fig. 4) has an elongated stalk ca. 2.5 times longer than the breadth and ca. 6 times longer than the depth; the greatest length recorded was 2.8 mm (Anderson, 1960). Three well-developed ossified processes are present, one median and two lateral. The median process is half the length of the stalk, curved with a broad base, and with a keel on the ventral side, and three lobes on the posterior side (Anderson, 1960). The lateral processes are large, distally flattened, and curved; the length is >33% the length of the stalk. The distal portion of the shaft is slender, broadening proximally to a terminal inflation. The dorsal concavity at the proximal end is deeper than the ventral (Anderson, 1960).

Clethrionomys californicus has relatively large sebaceous glands, poorly developed or atrophic sudoriferous glands, and intermediate mucous glands (Quay, 1965). In C. californicus, sudoriferous glands occur in the angulus oris, two on each side, on with its coiled (secretory) portion lying more dorsolaterally than the other (Quay, 1962). The more dorsolateral gland joins a hair follicle that extends anteromedially and opens into the oral vestibule, and the other gland joins a hair follicle that extends anterolaterally and opens just external to the angulus (Quay, 1962).

In Clethrionomys, including C. californicus, insertion of occipitoscapularis muscle in the forelimb is restricted to the cranial portion of the vertebral border; insertion of the omocervicalis muscle is restricted to the metacromion process; insertion of the biceps brachii muscle is mostly ulnar; and the abductor pollicis longus muscle has three points of insertion. Insertion of the femorococcygeus muscle in the hind limb extends along the distal end of the posterior femoral shaft; the two heads of the rectus femoris muscle have poorly defined tendons; the caudofemoralis muscle is beneath the deep surface of the femorococcygeus muscle (Stein, 1986, 1987).

ONTOGENY AND REPRODUCTION. Clethrionomys californicus on the west slope of the Cascade Mountains in northern Oregon breeds from February to November (Gashwiler, 1977). Males



Fig. 1. Photograph of juvenile female Clethrionomys californicus from 8 miles N, 1.5 miles E Alsea, Benton Co., Oregon (T12S, R7W, SW1/4 Sec. 29).

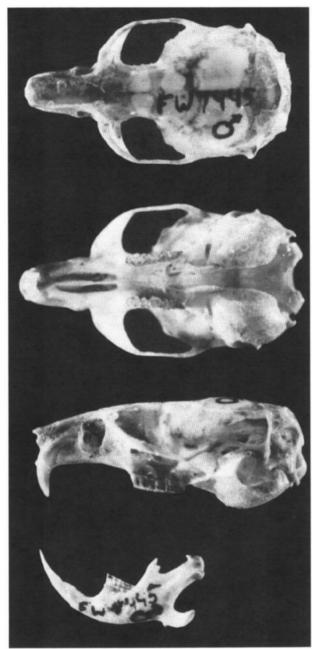


Fig. 2. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of an adult *Clethrionomys californicus* (Oregon State University, Department of Fisheries and Wildlife mammal collection 7445) from 10 miles NE Blue River, Lane Co., Oregon (T15S, R5E, Sec. 35). Occipitonasal length of skull is 24.53

with large (≥8.0 mm long), pink, and turgid testes, and tubules in cauda epididymides visible to the unaided eye were considered in breeding condition (Gashwiler, 1977). Males began to enter breeding condition in February (25% of 8) and all (n = 38) collected March-August were so considered; by September, numbers in breeding condition had begun to decline (88% of 16) and only a few breeding males were found in October (22% of 37). Females that contained embryos or were lactating were considered in breeding condition; 97% of 36 collected April-August were in breeding condition, but by September numbers of breeding females had declined (79% of 24) and only a few (18% of 17) remained in breeding condition until November. Natural deaths of overwintering animals compensated for early births so that the population did not increase noticeably until young born early in the year matured and became part of the breeding population (Gashwiler, 1959, 1977). More juveniles and

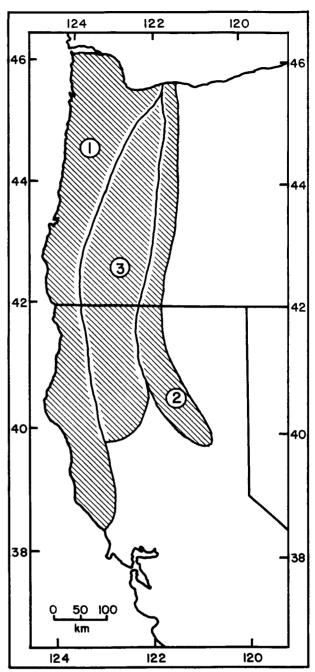


Fig. 3. Distribution of *Clethrionomys californicus*. Subspecies are: 1, *C. c. californicus*; 2, *C. c. mazama*; and 3, *C. c. obscurus*. Modified after Hall (1981).

more females in breeding condition were captured in riparian areas than in upland areas (Doyle, 1990). Western red-backed voles west of the Cascade Mountains breed throughout the year, because "Females that showed signs of having given birth (placental scars) and of nursing (development of the mammary glands) were caught in December, January, February, and March" (Maser et al., 1981: 198). MacNab and Dirks (1941) reported a pregnant female trapped on 19 July 1897 by A. K. Fisher that contained two embryos averaging 10 mm in diameter, and another they caught in 1937 contained four embryos averaging 3 mm in diameter.

Litter size for *C. californicus* averaged 2.86 (range, 2-7; n = 81) by counts of corpora lutea, 2.91 (range, 1-7; n = 57) by counts of pigmented sites of implantation, and 2.63 (range, 1-4; n = 24) by counts of embryos (Gashwiler, 1977). Four of the 24 pregnant females trapped also were lactating, suggesting that  $\geq 17\%$  of the females bred soon after giving birth. This is a minimum value

because early stages of pregnancy are not discernable (Gashwiler, 1977).

The gestation period of *C. californicus* averages 18 days (Palmer, 1954) with a range of 17–21 days (Maser et al., 1981). Gashwiler (1977) used a model to estimate that *C. californicus* has 3.1 litters/year; however, this is a low estimate because his samples for July and August contained no pregnant females. He obtained an estimate of 4.6 litters/year by use of the June percentage of pregnancies for July and the September percentage of pregnancies for August. Young of *C. californicus* have not been described in detail. Roest (1951) documented seeing an adult *C. californicus* carry a hairless young across a trail.

ECOLOGY. Clethrionomys californicus lives in a variety of forest habitats including closed-canopy, mature coniferous forest containing old fallen logs (Doyle, 1987; Gashwiler, 1959; Maser and Maser, 1988; Maser et al., 1981; Tevis, 1956). Old fallen logs in a closed-canopy forest typified by mesic conditions are an ideal location for growth of hypogeous fungi, a staple in the diet of C. californicus (Maser and Maser, 1988). C. californicus also inhabits 'open areas with thick duff and sound, downed wood" (Maguire, 1983:3426-B), redwood (Sequoia sempervirens) forests (Stephens, 1906) and in "mixed second growth fir-oak forest" (Easton, 1983: 216). C. californicus in the Coast Range of Oregon occurs in immature and mature conifer (lodgepole pine [Pinus contorta]rhododendron [Rhododendron macrophyllum] and Sitka spruce [Picea sitchensis]-salal [Gaultheria shallon]) forest and cedar (Thuja plicata)-swamp areas (Maser et al., 1981). Other Coast Range habitats include such species as Oregon big-leaf maple (Acer macrophyllum), Oregon alder (Alnus oregana), huckleberry (Vaccinium ovalifolium), bracken (Pteridium aquilinum pubescens), salmonberry (Rubus spectabilis), thimble berry (Rubus parvifloris), devil's club (Echinopanax horridum), vanilla-leaf (Achlys triphylla), false Solomon's seal (Vagnera sessilifolia), Oregon oxalis (Oxalis oregana), bride's bonnet (Clintonia uniflora), and fairy lantern (Disporum smithii - MacNab and Dirks, 1941). On the west slope of the Cascade Mountains of Oregon, C. californicus occurs in Douglasfir (Pseudotsuga menziesii) forests that include other conifers such as western hemlock (Tsuga heterophylla) and western red cedar and understory vegetation such as mountain Oregon grape (Berberis nervosa), salal, vine maple (Acer circinatum), wild blackberry (Rubus macropetalus), huckleberry (Vaccinium parvifolium), rhododendron, snow bramble (Rubus nivalis), Pacific yew (Taxus brevifolia), prince's pine (Chimaphila umbellata), gold thread (Coptis laciniata), twin-flower (Linnea borealis), sword fern (Polystichum munitum), rattlesnake plantain (Goodyera oblongifolia), violet (Viola sempervirens), starflower (Trientalis europaea), cool-wart (Tiarella unifoliata), whipplea (Whipplea modesta), inside-out-flower (Vancouveria hexandra), meadow-rue (Thalictrum occidentale), and lady fern (Athyrium felix-femina-Gashwiler, 1959, 1970), and silver fir (Abies amabilis), grand fir (Abies grandis), and red alder (Alnus rubra-Doyle, 1987). Farther east in the Cascade Mountains of Oregon, the overstory also may contain white fir (Abies concolor) and ponderosa pine (Pinus ponderosa — Hayes and Cross, 1987). In California, C. californicus reportedly occurs in brushlands of manzanita (Arctostaphylos sp.) and silktassel (Garrya sp.) during years of abundance (Jameson and Peeters, 1988).

The amount of light reaching the forest floor is related directly to whether or not C. californicus is present because this influences the quantity and quality of herbaceous material (Maser et al., 1981). Because C. californicus occurs more frequently in dense forest with little or no undergrowth, population densities are greater in forests with less light. With equal effort, significantly more western redbacked voles were captured in upland regions (n=203) than in riparian areas (n=82); also, with the same effort, more were captured in old-growth stands (>250 years old, n=227) than in mature stands (ca. 100 years old, n=58—Doyle, 1987). Habitats used by C. californicus (as opposed to those not used) were characterized by greater percentage cover of lichen, canopy cover of western hemlock, and total length of decaying logs, and lesser percentage cover of deciduous trees (Doyle, 1987).

Although C. californicus is associated closely with fallen logs (Doyle, 1987; Gashwiler, 1959; Maser et al., 1981; Tevis, 1956), the size and condition of logs may affect abundance. Logs with large diameters and large overhang areas are used more frequently (Hayes and Cross, 1987). Total captures/log were correlated significantly with both overhang width and maximum diameter of logs (Hayes,

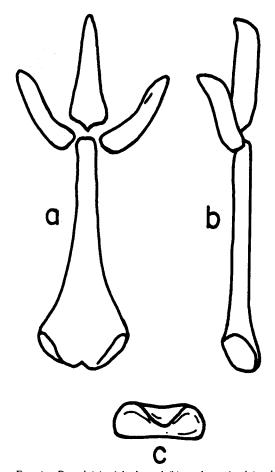


Fig. 4. Dorsal (a), right lateral (b), and proximal (c; dorsal surface upward) views of baculum of *Clethrionomys californicus*. Redrawn from Anderson (1960).

1983). C. californicus uses log overhangs as travel routes and perhaps as cover to avoid predators (Hayes and Cross, 1987). Number of captures was not correlated significantly with percentage of cover by moss or bark and number of voles captured was not correlated with state of decay of logs (Hayes and Cross, 1987). In contrast, Doyle (1987) determined that the abundance of western red-backed voles increased with an increase in abundance of old, decaying logs. She attributed this to the high concentrations of mycorrhizae in old logs. Decaying logs and sound logs may be used for different purposes by C. californicus; soft decaying logs may be used for foraging, nesting, or internal travel routes, whereas sound logs may be used for travel corridors and protection from predators (Hayes, 1983; Hayes and Cross, 1987).

After logging and burning, forested areas of the Pacific Northwest are no longer suitable habitat for C. californicus (Black and Hooven, 1974; Gashwiler, 1959, 1970; Hayes, 1983; Hooven and Black, 1976; Tevis, 1956). Estimated numbers (Lincoln Index) of C. californicus in virgin forest in western Oregon in 1954 ranged from 1.2 to 7.9/ha; a month before logging in June 1955, density was estimated to be 4.9/ha and 2 months after logging the estimate was 5.4/ha (Gashwiler, 1959). Before slash was burned in October the estimate was 12.4/ha, but immediately after the burn there were only 4.7/ha; the November estimate increased to 7.4 voles/ ha. However, the following spring (1956) no Clethrionomys was trapped on the area on which slash was burned. Apparently, burning removed enough of the logs that supplied food and cover to make the area unattractive and western red-backed voles either moved, died, or both (Gashwiler, 1959). C. californicus was not captured for 7 years in unburned portions within a 17,500-ha area devastated by wildfire (Black and Hooven, 1974). As these voles generally are found in cool, moist microhabitats in the deep forest, higher ground temperatures resulting from removal of cover possibly contributed to the disappearance of C. californicus (Gashwiler, 1970). A similar association of abundance of C. californicus and forest cutting or

slash-burning practices was reported in the Cascade Mountains of Oregon and Klamath Mountains of California (Hooven and Black, 1976; Maguire, 1983). Although logging has a deleterious effect on populations of *C. californicus*, it does not seem to be as immediate or as drastic as that resulting from slash burning (Gashwiler, 1959). Such effects may be related to differences in impact that logging and burning have on fungi (or their hosts) used by western redbacked voles for food (Hayes, 1983; Maser et al., 1978a).

In the H. J. Andrews Experimental Forest, Lane and Linn counties, Oregon, C. californicus had a sex ratio of 1:1.26 (n=97) in favor of males; this sample combined with a sample (n=161) from the same area and from Mt. Hood National Forest, Clackamas Co. (sex ratio, 1:0.81) produced an overall sex ratio of 1:0.95 (Gashwiler, 1959, 1977). Samples for February, March, and August were dominated by males, whereas those for January, April, and December were dominated by females. In the Cascade Mountains (Hooven, 1971) and the Coast Range (MacNab and Dirks, 1941) of Oregon, sex ratios in small samples (n=15-49) favored males (1:1.4-1.7).

As succession proceeds from the grass-forb-brush stage toward young forest, *C. californicus* becomes more abundant and *Microtus oregoni* becomes less abundant (Maser et al., 1978b). During intermediate stages, these voles coexist because a supply of hypogeous fungi is present for *C. californicus* and some grasses and forbs persist for *M. oregoni*. Thus, the successional stage of the forest affects interspecies competition for habitat.

In western Oregon and northwestern California, C. californicus composed a larger proportion of small mammals trapped along county-road rights-of-way than along interstate rights-of-way (Adams and Geis, 1983). Most western red-backed voles along roadways were trapped in Douglas-fir, but a few were caught in other habitats including Oregon white oak (Quercus garryana).

In Oregon, the diet of *C. californicus* consisted largely of fungal sporocarps and lichens; the composition did not vary significantly by month in the Coast Range, but sporocarps disappeared from the diet during winter and early spring in the Cascade Mountains. Hypogeous fungi, comprising 95% of all sporocarps eaten, generally are not available in summer but continue to occur in stomach contents of *C. californicus*; thus, *C. californicus* may cache supplies. Miscellaneous food items eaten by *C. californicus* include conifer seeds during seed fall and occasionally insect larvae (Ure and Maser, 1982).

Of 19 genera of fungal spores identified in fecal pellets of C. californicus in southern Oregon, the most common were those of Rhizopogon and Gautieria (Hayes, 1983; Hayes et al., 1986). Rhizopogon, Gautieria, Hysterangium, and Leucogaster were found nearly all year and Hymenogaster, Calvatia, Hydnotyra, Melanogaster, Tuber, Martellia, and Octavianina were found in significant amounts during overlapping periods of 3-6 months at different times during the year (Hayes, 1983; Hayes et al., 1986). Microthecium, Geopora, Genea, Elaphomyces, Endogone, Gastroboletus, Genabea, and Glomus occurred infrequently (Hayes, 1983; Hayes et al., 1986). Feces of a C. californicus contained Azospirillum sp., a nitrogen-fixing bacterium capable of surviving passage through the digestive tract of this and other species of small mammals (Li et al., 1986). Thus, C. californicus may serve to disseminate spores of hypogeous fungi and bacteria that contribute significantly to certain forest ecosystems.

The diet of western red-backed voles is related to their habitat (Maser and Maser, 1988; Ure and Maser, 1982). Individuals found at higher elevation are subjected to more drastic climatic changes, consequently, their diet is more variable than that of individuals at lower elevations. Where temperatures cool earlier in the year, the fungal fruiting season is abbreviated, thus, use of lichens by these voles is more common at higher elevations than at lower elevations (Hayes et al., 1986; Ure and Maser, 1982).

Syntopic terrestrial mammal associates of C. californicus include: Sorex bairdi, S. pacificus, S. sonomae, S. trowbridgii, S. vagrans, Neurotrichus gibbsii, Scapanus orarius, Microtus longicaudus, M. oregoni, M. richardsoni, Peromyscus maniculatus, P. truei, Phenacomys albipes, P. intermedius, Zapus trinotatus, Neotoma cinerea, N. fuscipes, Tamias amoenus, T. townsendii, Tamiasciurus douglasii, Spermophilus lateralis, Sciurus griseus, Glaucomys sabrinus, Aplodontia rufa, Thomomys mazama, Ochotona princeps, Lepus americanus, Didelphis virginiana, Erethizon dorsatum, Spilogale gracilis, Mustela erminea, M. frenata, Martes americana, Canis latrans, Ursus americanus, Procyon

lotor, Felis rufus, Cervus elaphus, and Odocoileus hemionus (Black and Hooven, 1974; Carraway, 1990; Doyle, 1987, 1990; Easton, 1983; Franklin et al., 1981; Gashwiler, 1959, 1970; Gresbrink and Hopkins, 1982; Hooven and Black, 1976; Ingles, 1954; Maguire, 1983; Maser et al., 1978a, 1981; McIntire, 1985; Moore, 1942; Nussbaum and Maser, 1975; Tevis, 1956; Ure and Maser, 1982; West, 1985). Other species may be associated with C. californicus but such has not been documented.

Clethrionomys californicus is preyed on by martens (Martes americana), ermines (Mustela erminea), long-tailed weasels (Mustela frenata), spotted skunks (Spilogale gracilis), and feral domestic cats (Felis silvestris—Maser et al., 1981). Remains were found in pellets of the saw-whet owl (Aegolius acadicus—Forsman and Maser, 1970) and northern spotted owl (Strix occidentalis—Forsman, 1975, 1980). In western Oregon, C. californicus occurred with a frequency of 1.1-5.3% and 0-6.2% in fecal samples from bobcats (Felis rufus) and coyotes (Canis latrans), respectively (Nussbaum and Maser, 1975; Witmer and deCalesta, 1986); highest values occurred during summer-fall.

Clethrionomys californicus has been captured in large Sherman live traps baited with cracked corn, wheat, oats, and sometimes barley (Gashwiler, 1959, 1970). In addition, C. californicus has been captured in household and museum special kill traps, and in unbaited pitfalls (Gashwiler, 1977; Ure and Maser, 1982; West, 1985). Rates of capture of C. californicus in old and new style museum specials were not significantly different (West, 1985).

Ectoparasites of C. californicus include chiggers (Acari): (Trombiculidae) Chatia setosa, Euschoengastia oregonensis, Neotrombicula cavicola, N. harperi (Easton, 1975); mites (Acari): (Cyrtolaelapidae) Cyrtolaelaps sp. (Whitaker and Maser, 1984); (Glycyphagidae) Glycyphagus hypudaei; (Laelapidae) Androlaelaps fahrenholzi, Echinonyssus isabellinus, E. obsoletus, Eulaelaps stabularis, Haemogamasus occidentalis, H. reidi, Haemogamasus sp.; (Listrophoridae) Listrophorus mexicanus (Whitaker and Maser, 1984, 1985); (Macrochelidae-Whitaker and Maser, 1984); (Mycoptidae) Myocoptes japonensis; (Myobiidae) Protomyobis brevisetosa; (Pygmephoridae) Bakerdania sp. (Whitaker and Maser, 1984); Pygmephorus designatus (Whitaker and Maser, 1984, 1985); (Rhodacaridae) Euryparasitus sp. (Whitaker and Maser, 1984); fleas (Siphonaptera): Atyphloceras m. multidentatus (Easton, 1983), Catallagia chamberlini (Gresbrink and Hopkins, 1982; Hubbard, 1941, 1947), C. sculleni, Catallagia sp. (Gresbrink and Hopkins, 1982), Leptopsylla selenis (Hubbard, 1941), Malaraeus telchinum (Gresbrink and Hopkins, 1982; Hubbard, 1941, 1947), Malaraeus sp. (Gresbrink and Hopkins, 1982), Monopsyllus wagneri (Easton, 1983; Hubbard, 1947), Opisodasys keeni (Hubbard, 1941), Orchopeas sexdentatus, Oropsylla idahoensis (Gresbrink and Hopkins, 1982), Peromyscopsylla selensis (Gresbrink and Hopkins, 1982; Hubbard, 1943, 1947), Peromyscopsylla sp. (Gresbrink and Hopkins, 1982).

BEHAVIOR. Circular home ranges based on radii encompassing 95% of capture points (Hooven, 1958) were 4.6 ha for males (n = 12) and 0.8 ha for females (n = 8—Hooven, 1971). There has been little other documented information on C. californicus behavior; that available is largely anecdotal. Western redbacked voles build nests underground in burrows, under logs, or under old leaves (Stephens, 1906) and forage mostly under the surface of the forest floor where the temperature is more stable than that of the aboveground environment (Maser et al., 1981). Weather may influence aboveground activity of C. californicus (Maguire, 1983; Maser et al., 1981). C. californicus in the Cascade Mountains is mainly nocturnal whereas in the Coast Range it is active at any time (Maser et al., 1981). One western red-backed vole was "... seen in bright sunlight ..." in the vicinity of the Oregon Caves National Monument (Roest, 1951:348).

GENETICS. Clethrionomys californicus has a diploid chromosome number of 56 with 26 pairs of somatic acrocentrics and one pair of somatic metacentrics. The X chromosome is large and acrocentric, the Y is tiny. The size of the Y chromosome in C. californicus apparently is unique within the genus Clethrionomys (Modi, 1985).

REMARKS. Merriam (1890, 1897) considered occidentalis, californicus, obscurus, and mazama as specifically different within the genus Evotomys. Palmer (1928) applied the European generic name Clethrionomys to all New World red-backed voles. Grinnell

(1933) decided that mazama and obscurus were conspecific with mazama having page priority (Merriam, 1897). Bailey (1936) considered all red-backed voles in western Oregon to be C. californicus. Dalquest (1948) considered C. californicus and C. occidentalis to be conspecific within C. californicus without comment; however, Hall and Cockrum (1952) concluded that C. occidentalis has page priority from Merriam's (1890) original account and renamed all C. occidentalis. Johnson and Ostenson (1959) separated C. occidentalis and C. californicus at the Columbia River. Modi (1985) indicated that the unique Y chromosome supports Johnson and Ostenson's (1959) separation of C. occidentalis and C. californicus.

The generic name *Clethrionomys* is from the Greek *kleithrion* meaning "a bar for closing" and *myos* meaning "mouse"; the specific name *californicus* is from the state of California in which the type specimen was collected (Jaeger, 1955).

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- L. F. ALEXANDER AND B. J. VERTS, DEPARTMENT OF FISHERIES AND WILDLIFE, OREGON STATE UNIVERSITY, CORVALLIS, OREGON 97331.