

Microtus longicaudus. By Michael J. Smolen and Barry L. Keller

Published 27 February 1987 by The American Society of Mammalogists

Microtus longicaudus (Merriam, 1888)

Long-tailed Vole

- Arvicola (Mynomes) longicaudus* Merriam, 1888:934. Type locality Custer, 5,500 ft, Black Hills, Custer Co., South Dakota.
- Arvicola (Mynomes) alticolus* Merriam, 1890:67. Type locality Little Spring, 8,200 ft, San Francisco Mountains, Coconino Co., Arizona.
- Arvicola (Mynomes) mordax* Merriam, 1891:61. Type locality Sawtooth (or Alturus) Lake, 7,200 ft, east base of Sawtooth Mountains, Blaine Co., Idaho.
- Arvicola leucophaeus* Allen, 1894:320. Type locality Graham Mountains, Graham Co., Arizona.
- Microtus angusticeps* Bailey, 1898:86. Type locality Crescent City, Del Norte Co., California.
- Microtus macrurus* Merriam, 1898:353. Type locality Lakeushman, Olympic Mountains, Mason Co., Washington.
- Microtus vellerosus* Allen, 1899:7. Type locality upper Liard River, British Columbia.
- Microtus cautus* Allen, 1899:7. Type locality Hell's Gate, Liard River, British Columbia.

CONTENT AND CONTEXT. Order Rodentia, Family Muridae, Subfamily Arvicolinae (Carleton and Musser, 1984), Genus *Microtus*, Subgenus *Microtus*. The subgenus contains 12 extant species in the Nearctic (Hall and Cockrum, 1953). The species *Microtus longicaudus* contains 14 subspecies (Hall, 1981) as follows:

- M. l. abditus* Howell, 1923:36. Type locality Walker's Ranch, Pleasant Valley, 8 mi S Tillamook, Tillamook Co., Oregon.
- M. l. alticola* (Merriam), 1890:67, see above.
- M. l. angusticeps* Bailey, 1898:86, see above.
- M. l. baileyi* Goldman, 1938:492. Type locality Greenland Spring, head of Bright Angel Creek, 8,000 ft, Grand Canyon National Park, Coconino Co., Arizona.
- M. l. bernardinus* Merriam, 1908:145. Type locality Dry Lake, 9,000 ft, at north base San Geronio Peak, San Bernardino Mountains, San Bernardino Co., California.
- M. l. halli* Hayman and Holt, 1941:603. New name for *Microtus mordax angustus* Hall, 1931:13. Type locality Godman (=Goodman, Hall, 1981) Springs, 5,700 ft, Blue Mountains, Columbia Co., Washington.
- M. l. incanus* Lee and Durrant, 1960:168. Type locality ¼ mi SE Burned Ridge, Mount Ellen, Henry Mountains, 10,300 ft, Garfield Co., Utah.
- M. l. latus* Hall, 1931:12. Type locality Wisconsin Creek, 8,500 ft, Toyabe Mountains, Nye Co., Nevada.
- M. l. leucophaeus* (Allen), 1894:320, see above.
- M. l. littoralis* Swarth, 1933:209. Type locality Shaken, Prince of Wales Island, Alaska. Hall (1981) noted a discrepancy in this type locality, namely that Shaken is located on Kosciusko Island, and proposed that the locality should be Prince of Wales Island, opposite Shaken.
- M. l. longicaudus* (Merriam), 1888:934, see above (*mordax* Merriam a synonym).
- M. l. macrurus* Merriam, 1898:353, see above.
- M. l. sierrae* Kellogg, 1922:288. Type locality Tuolumne Meadows, Yosemite National Park, 8,600 ft, Tuolumne Co., California.
- M. l. vellerosus* Allen, 1899:7, see above (*cautus* Allen a synonym).

DIAGNOSIS. The subgenus *Microtus* differs from *Herpetomys*, *Pedomys*, *Pitymys*, *Orthromys*, *Chilotus*, and *Aulacomys* in having six plantar tubercles whereas the others have five. *Stenocranium* likewise has six plantar tubercles, but differs in having a narrower skull with a pronounced median crest and a third lower molar (m3) with two closed and one open triangles. *Microtus* also

differs from *Herpetomys* and *Orthromys* in that the m3 of *Microtus* has three transverse loops and no closed triangles instead of two transverse loops and two median triangles. The three closed triangles of the m3 and eight mammae of *Microtus* separate it from the subgenera *Pitymys* and *Pedomys* that have m3 with two closed triangles and four or six mammae (Bailey, 1900; Hall and Cockrum, 1953).

The long tail, incisive foramina, and nasals of *M. longicaudus* are useful in distinguishing them from other species in the subgenus. The relatively long tail in relation to head and body length and hindfoot length separates *M. longicaudus* from most other species of *Microtus*. The head and body length of *M. longicaudus* is from 1.6 to 1.9 times as long as the tail, and the tail is from 2.8 to 3.5 times the length of the hindfoot. Only *M. californicus* (2.0-2.5 times tail length; 2.3-2.6 times length of hindfoot), *M. pennsylvanicus* (2.0-3.1 × tail length; 1.9-2.7 × length of hindfoot), and *M. townsendii* (2.2-2.4 × tail length; 2.2-2.6 times length of hindfoot) have head and body to tail or tail to hindfoot proportions that approximate those of *M. longicaudus* (Hall and Cockrum, 1953). The four closed triangles in M2 of *M. longicaudus* distinguishes it from *M. pennsylvanicus* that has an M2 with five closed triangles. Incisors are hidden by nasals when viewed from above in *M. longicaudus* rather than being visible as in *M. townsendii*. Furthermore, the incisive foramina are tapered gradually or at least as wide posteriorly as anteriorly in *M. longicaudus* whereas the foramina are long, narrow, and constricted posteriorly in *M. townsendii*. *Microtus californicus* is more difficult to separate if tail-length proportions are not definitive (Maser and Storm, 1970).

GENERAL CHARACTERS. *Microtus longicaudus* is a small, thick-bodied vole characterized by a long, bicolored tail that is greater than one-third the total length of the animal (Fig. 1). Pelage color ranges from dull grayish through brownish gray to dark sepia brown. Numerous black tipped hairs occur on the dorsal and lateral portions of the animal. The sides are more grayish and the ventral surface varies from grayish-white to a dull buff (Hall and Cockrum, 1953). Ears are large and haired, and eyes are large. There are four inguinal and four pectoral mammae. The skull is long and flattened (Fig. 2). The braincase is wide and bullae are large and round. The rostrum is long (Bailey, 1900; Hall and Cockrum, 1953; Maser and Storm, 1970).

The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16 (Fig. 3). The m1 has a distinct anterior cap with two shallow reentrant angles and one confluent pool of dentine, and is followed by five triangles each with their own isolated dentine pool (terminology that of van der Meulen, 1978). The posterior lobe is crescent-shaped and directly adjoins m2. The m2 consists of four separated



FIG. 1. *Microtus longicaudus abditus* collected from Miami River, Tillamook Co., Oregon. Photograph provided by Murray L. Johnson.

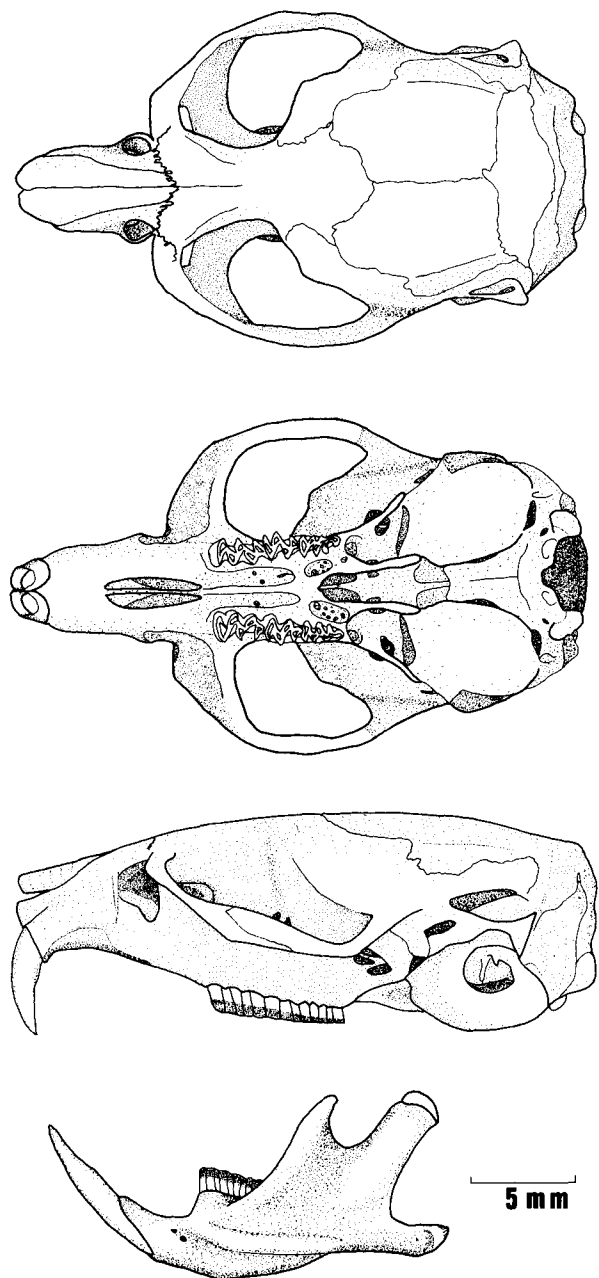


FIG. 2. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw of *Microtus longicaudus longicaudus*, TCWC 25119, male from 5 mi ENE New Meadows, Adams Co., Idaho.

triangles and a posterior lobe. The m3 consists of three crescent-shaped triangles. The M1 has an anterior spherical triangle, and is followed by four closed triangles. The M2 resembles M1 but lacks a triangle. The M3 has a spherical triangle that is followed by two closed triangles. The posterior portion of M3 is variable and consists of a triangle and a large posterior crescent that may have confluent pools of dentine.

Means and ranges (in parentheses) of external measurements (in mm), and sample sizes, are recorded for adults for the following subspecies: *M. l. alticola* (Utah; Durrant, 1952) males followed by females, total length, 175 (169 to 179) 4 and 172 (164 to 180) 6; length of tail, 56.5 (52 to 60) 4 and 57 (56 to 60) 6; length of hind foot, 20.5 (20 to 21) 4 and 20 (19 to 21) 6; length of ear, 14 (13 to 15) 4 and 14 (13 to 15) 6; *M. l. angusticeps* (California; Kellogg, 1922) males and females combined, total length, 174.3 (162 to 194) 10; length of tail, 61.2 (56 to 74) 10; length of hind foot, 22.0 (21 to 23) 10; *M. l. bernardinus* (California; Kellogg, 1922) males and females combined, total length 183.8 (170 to 198) 10; length of tail, 62.6 (53 to 68) 10; length of hind foot, 22.4 (21

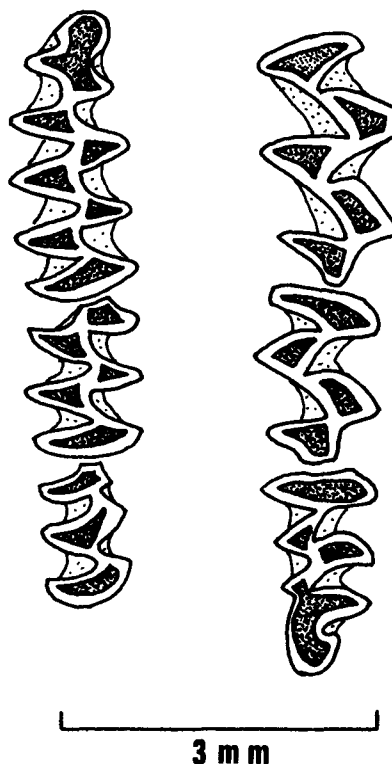


FIG. 3. Occlusal view of right lower (on left with lingual side to the left) and right upper (on right with lingual side to the right) molar tooth rows. Anterior is at the top, dentine is black, enamel is open, and cement is lightly stippled. TCWC 25119, male collected from 5 mi ENE New Meadow, Adams Co., Idaho.

to 23) 10; *M. l. incanus* (Utah; Lee and Durrant, 1960) males followed by females, total length, 172.6 (162 to 182) 5 and 170.4 (155 to 186) 12; length of tail, 52.8 (49 to 59) 5 and 53.1 (49 to 58) 12; length of hind foot, 21.4 (21 to 22) 5 and 21.1 (19 to 24) 12; length of ear, 14.0 (13 to 15) 5 and 14.3 (13 to 15) 12; *M. l. latus* (Utah; Hall, 1931) males and females combined, total length, 187 (180 to 197) 10; length of tail, 60 (52 to 70) 10; length of hind foot, 22.4 (21 to 24) 10; *M. l. leucophaeus* (Arizona; Hoffmeister, 1956) males ($n = 12$) followed by females ($n = 8$), total length, 171.6, 184.9; length of tail, 52.8, 57.9; length of hind foot, 22.3, 21.9; length of ear, 15.8, 15.8; *M. l. longicaudus* (Nevada; Borell and Ellis, 1934) males followed by females, total length, 187 (174 to 196) 10 and 185 (171 to 197) 10; length of tail, 64 (57 to 68) 10 and 63 (57 to 70) 10; length of hind foot, 21.2 (20 to 22) 10 and 20.9 (20 to 22) 10; *M. l. macrurus* (British Columbia; Anderson and Rand, 1944) males only, total length 197.6 (191 to 202) 5; length of tail 77.0 (70 to 81) 5; length of hind foot 22.7 (21.5 to 23.5) 5; *M. l. sierrae* (California; Kellogg, 1922) males and females combined, total length, 196.0 (190 to 221) 51; length of tail, 68.4 (55 to 77) 51; length of hind foot, 22.2 (21 to 24) 51; *M. l. vellerous* (British Columbia; Allen, 1903) males followed by females, total length, 175.3 (158 to 190) 6 and 176 (160 to 195) 21; length of tail, 61.3 (52 to 70) 6 and 60.6 (50 to 70) 21; length of hind foot, 20.8 (19 to 21) 6 and 21 (19.5 to 21.5) 21; length of ear, 14 (13 to 15) 6 and 14 (13 to 15) 21.

Means and ranges (in parentheses) of body mass (in g) and sample sizes for *M. l. latus* are as follows: males followed by females, 47.3 (39.0 to 56.8) 10 and 49.4 (46.0 to 58.4) 6; and for *M. l. longicaudus*, 46.5 (36.9 to 56.9) 10 and 46.9 (42.0 to 51.2) 10 from Nevada (Hall, 1946).

Means and ranges of cranial measurements (in mm) for 10 male and 10 female (respectively) *M. l. longicaudus* from Nevada (Hall, 1946) are: condylobasal length, 26.8 (25.6 to 27.7), 26.8 (25.6 to 28.4); occipitonasal length, 26.9 (26.3 to 27.7), 27.0 (26.2 to 28.6); nasal length, 7.8 (7.4 to 8.1), 7.8 (7.1 to 8.1); zygomatic breadth, 15.3 (14.5 to 16.0), 15.2 (14.0 to 16.0); interorbital breadth 3.7 (3.5 to 3.9), 3.6 (3.5 to 3.8); mastoid breadth, 12.3 (11.8 to 12.7), 12.2 (11.5 to 13.2); alveolar length, 6.5 (6.2 to 6.9), 6.6 (6.2 to 6.9); rostrum width, 5.3 (5.0 to 5.5), 5.1 (4.7 to

5.3); palatilar length, 13.2 (12.0 to 13.8), 13.3 (12.5 to 13.9); width of auditory bullae, 6.0 (5.7 to 6.3), 6.2 (5.5 to 6.5). Cranial measurements for the other subspecies are contained in the following: *M. l. angusticeps* (Kellogg, 1922), *M. l. bernardinus* (Kellogg, 1922), *M. l. incanus* (Lee and Durrant, 1960), *M. l. latus* (Hall, 1946), *M. l. leucophaeus* (Hoffmeister, 1956), and *M. l. sierrae* (Kellogg, 1922). There is no significant size dimorphism between the sexes, although males average slightly larger than females in length of hind foot and eight cranial measurements (Hall, 1946; Turner, 1974).

DISTRIBUTION. *Microtus longicaudus* occurs throughout most of western United States and Canada to eastern Alaska (Fig. 4). The eastern and southern boundaries usually consist of populations in coniferous forests restricted to high elevations of isolated mountains. The eastward extension into the Great Plains occurred in the Pleistocene (Hoffmann and Jones, 1970; Turner, 1974), and subsequent warming and floral changes associated with increased aridity stranded populations in the Big Belt, Crazy, Little Belt, Big Snowy, Laramie, and Big Horn mountains (Hoffmann and Jones, 1970) and Black Hills (Hoffmann and Jones, 1970; Turner, 1974). Similar isolations are believed to account for *M. l. incanus* (Lee and Durrant, 1960) being restricted to the Henry Mountains in Utah, and are suspected to account for the mountaintop populations occurring in the San Bernardino Mountains in California (Kellogg, 1922), and in the Sacramento, Mimbres, and Graham mountains in New Mexico and Arizona (Findley and Jones, 1962).

FOSSIL RECORD. Fossil remains of *M. longicaudus*, *M. montanus*, and *M. pennsylvanicus* are difficult to identify because of the similarity in their dental and cranial morphologies. Current records of long-tailed voles range from late Wisconsin to Recent, and their identifications usually are based on "geographic probability" and "faunal assemblages" (Guilday et al., 1977). These sites are: Idaho, Moonshiner Cave, Bingham Co. (White et al., 1984); Wyoming, Agate Basin Site, Niobrara Co. (Walker, 1982), Little Box Elder Cave, Converse Co. (Anderson, 1968); Colorado, Chimney Rock Animal Trap, Larimer Co. (Hager, 1972); New Mexico, Burnet Cave, Eddy Co. (Schultz and Howard, 1935), Dry Cave, Eddy Co. (Harris, 1970).

FORM. The structure of the baculum is similar to that of *M. pennsylvanicus* (Burt, 1960; Hooper and Hart, 1962), but differs in shaft proportions (Anderson, 1960). The proximal bone of the baculum is broad and straight. The basal shaft is broad and angular, and, when viewed from the end, is dumbbell-shaped with the greater concavity on the dorsal portion. The shaft tapers to a blunt point and has a cartilaginous connection with the three lateral segments that curve laterad and dorsad from the junction.

The dorsal lobe of the glans penis is elevated slightly above the ventral rim of the crater and is nonpapillose. The remaining portions of the rim bear between five and eight spine-tipped fingers per side. The urethral process consists of two unmistakable lobes that are curved laterally (Hooper and Hart, 1962).

An os clitoridis, when present, is situated anterodorsal to the urethra and well within the connective tissue of the clitoris (Ziegler, 1961). The structure is rod-shaped with each end slightly expanded and with only the distal half ossified.

Dental abnormalities are known. Jones (1978) reported distinct lateral grooves on the incisors of a female vole from the Yukon. Flattened incisors appeared in 10 voles, and various degrees of malocclusion of both incisors and molars were described in 11 other voles in Oregon (Maser and Hooven, 1970). Harris and Fleharty (1962) found an extra tooth in the right lower tooth row of a vole from New Mexico.

Although many mammalogists list the presence of hip glands as a characteristic of the subgenus *Microtus* (Bailey, 1900; Hall and Cockrum, 1953), *M. longicaudus* usually does not possess such glands (Quay, 1968). The development of hip glands can be induced with testosterone injections (Jannett, 1975).

Long-tailed voles have a mean of 4.5 and a mode of three meibomian glands in each eyelid (Quay, 1954).

FUNCTION. Mean diameter of erythrocytes is 6.3 μ (range = 5.1 to 7.0, $n = 11$). Hemoglobin concentration (g/100 ml), hematocrit ratio, and mean corpuscular hemoglobin concentrations for *M. longicaudus* from 2,895 m is as follows: adult males, ($n = 7$) 16.2, 49.4, 32.9; pregnant females, ($n = 4$) 15.8, 49.4, 32.0 (Sealand, 1964).

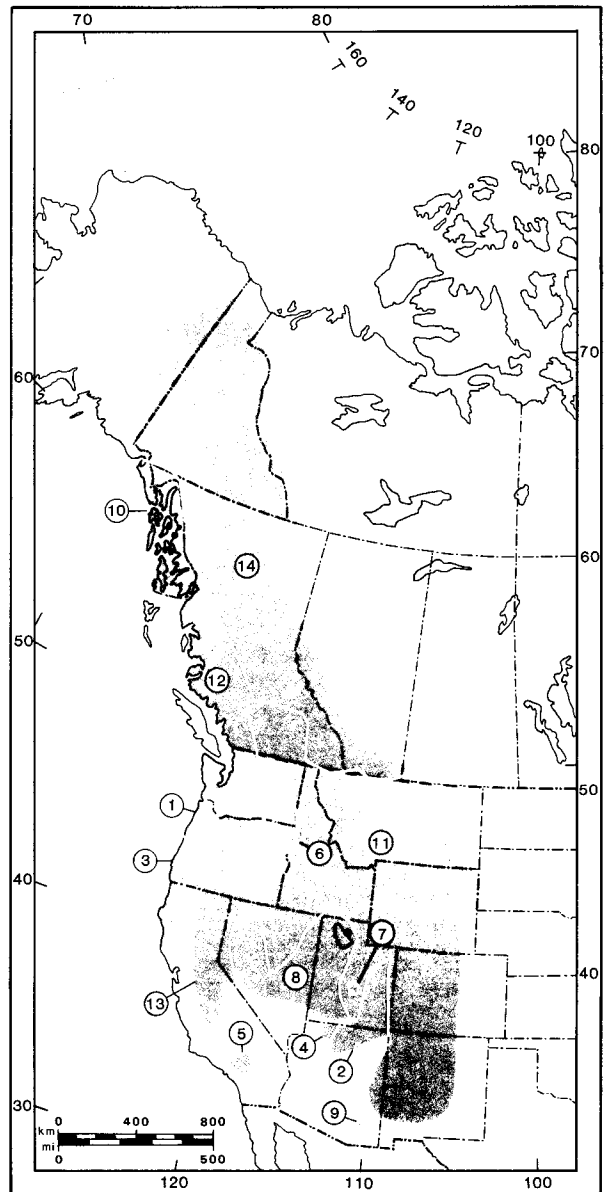


FIG. 4. Geographic distribution of the recognized subspecies of *Microtus longicaudus* (Hall, 1981): 1, *M. l. abditus*; 2, *M. l. alticola*; 3, *M. l. angusticeps*; 4, *M. l. baileyi*; 5, *M. l. bernardinus*; 6, *M. l. halli*; 7, *M. l. incanus*; 8, *M. l. latus*; 9, *M. l. leucophaeus*; 10, *M. l. littoralis*; 11, *M. l. longicaudus*; 12, *M. l. macrurus*; 13, *M. l. sierrae*; 14, *M. l. vellerosus*.

With the animal in nesting material, the thermoneutral zone was from 20° to 30°C, and the metabolic rate was 2.62 cc O₂ g⁻¹ h⁻¹. The thermoneutral zone extended from 25° to 30°C in animals outside of their nest, and mean body temperatures were 37.1°C at 5°C ambient air temperature, 37.5°C at 15°C, and 37.7°C at 25°C. Ambient temperatures above 32°C were lethal (Beck and Anthony, 1971).

ONTOGENY AND REPRODUCTION. The breeding season extends from May through October for populations in Nevada with most reproductive activity observed in June and July (Hall, 1946). Populations in Alaska have a breeding season from midMay to midSeptember (Van Horne, 1982), similar to that reported for Idaho (Davis, 1939).

Information concerning gestation, development, growth, and age at sexual maturity is lacking for long-tailed voles. The largest crown-rump measurement of an embryo was 24 mm (Long, 1940).

Mean litter sizes followed by the ranges (in parentheses) and sample sizes are: Arizona, 4.9 (4 to 6) 10 (Hoffmeister, 1956); Nevada, 5.6 (2 to 8) 39 (Hall, 1946); Wyoming, 6.0 (5 to 7) 3

(Clark, 1973); Black Hills, South Dakota and Wyoming, 4.7 (4 to 6) 15 (Turner, 1974); Alaska, 5.0 (no data) 26 (Van Horne, 1982); and a laboratory colony of Colorado stock, 5.3 (1 to 7) 6 (Colvin and Colvin, 1970).

Females produce a maximum of two litters in their life, and no voles were observed to survive to their second reproductive season in Alaska (Van Horne, 1982). Long-tailed voles seldom live longer than 1 year (Jenkins, 1948). Females lived longer than males; 13.5 months is the maximum observed age of two females (Van Horne, 1982).

ECOLOGY. Populations of *M. longicaudus* occur in a wide variety of habitats throughout their range, varying from spruce-fir (*Picea* sp.-*Abies* sp.) forests (Findley and Jones, 1962; Findley and Negus, 1953; Findley et al., 1975), thickets (Armstrong, 1977; Borell and Ellis, 1934; Findley and Negus, 1953; Randall, 1978; Rickard, 1960), forest-meadow ecotones (Findley and Jones, 1962; Findley et al., 1975), riparian zones (Armstrong, 1977; Borell and Ellis, 1934; Hoffmeister, 1956; Long, 1940; Turner, 1974) and grassy or sagebrush areas (Borell and Ellis, 1934; Brown, 1967; Hoffmeister, 1956; Linsdale, 1938; Randall, 1978; Stinson, 1978). Long-tailed voles are not found in old-growth forests in Montana, but are common in areas that were recently cut or burned (Halvorson, 1982).

Clear-cuttings in forests create favorable habitats in Alaska (Van Horne, 1983) and Alberta (Morris, 1984), whereas closed spruce (*Picea glauca*)-willow (*Salix glauca*), closed spruce-buffaloberry (*Shepherdia canadensis*), and open spruce-buffaloberry habitats support populations in the Yukon (Krebs and Wingate, 1976).

The shrubs snowberry (*Symphoricarpos albus*), pearhip wood's rose (*Rosa woodsii* var. *ultramontana*), Spalding's rose (*R. nutkana*), and chokeberry (*Prunus virginiana*), the grasses Idaho fescue (*Festuca idahoensis*), and bluebunch wheat grass (*Agropyron spicatum*), and the forbs one-flowered little sunflower (*Helianthella douglasii*), arrow-leaved balsamroot (*Balsamorhiza sagittata*), western hawkweed (*Hieracium albertinum*), and silky lupine (*Lupinus sericeus*) occur in habitats occupied by *M. longicaudus* in Washington (Beck and Anthony, 1971; Randall, 1978; Randall and Johnson, 1979) and Idaho (Rickard, 1960). Populations on the Malheur National Wildlife Refuge in Oregon are confined to marshes containing hardstem bullrush (*Scirpus acutus*), cattail (*Typha latifolia*), Baltic rush (*Juncus balticus*), and sedges (*Carex* sp.; Feldhamer, 1979). In Wyoming, long-tailed voles are found in wetter and structurally more complex areas (Clark, 1973), and are common to willow-alder (*Salix* sp.-*Alnus tenuifolia*), aspen (*Populus tremuloides*, with *Poa* sp. and *Agropyron* sp. understorey), and sedges and forbs in subalpine meadows (*Carex* sp., *Erigeron* sp., *Trifolium* sp., *Phlox* sp., and *Aguilegia* sp.; Brown, 1967). Grassy slopes in the lower montane zone in Colorado with ground cover consisting of shrubby cinquefoil (*Pentaphylloides floribunda*), wax currant (*Ribes cereum*), prairie sage (*Artemisia ludoviciana*), cheat grass (*Bromus tectorum*), blue gramma (*Bouteloua gracilis*), and Kentucky bluegrass (*Poa pratensis*) support vole populations (Stinson, 1978). Armstrong (1977) described *M. longicaudus* habitats as containing 31% willows, 20% logs, 17% spruce, 17% aspen (*Populus* sp.), and an understorey containing 77% forbs and 11% graminoids.

Habitats of long-tailed voles in New Mexico range from montane forests consisting of alders (*Alnus* sp.), cottonwoods (*Populus* sp.), willows from 2,468 m to 2,895 m (Hill, 1942) and spruce and fir forests (Findley and Jones, 1962). They also were found on grass and scrub hillsides (Findley and Jones, 1962), vegetated by Kentucky bluegrass, yarrow (*Achillea lanulosa*), vetch (*Vicia americana*), and bedstraw (*Galium asperillum*; Conley, 1976). *M. longicaudus* usually is restricted to scrubby and grassy meadows and flats above 2,438 m in Arizona (Hoffmeister, 1956). The relationship of long-tailed voles to water is not known precisely. The presence of standing water is not considered essential (Borell and Ellis, 1934) and individuals have been taken as far as 0.81 km from water in Nevada (Hall, 1946), whereas in New Mexico long-tailed voles required water for daily sustenance (Findley et al., 1975).

Diets of both sexes are nearly identical, and *M. longicaudus* consumed more fruits and seeds, followed by dicots, and lesser amounts of monocots (Van Horne, 1982). Stomach analysis of 14 Wyoming long-tailed voles consisted of 38% by volume (55% by occurrence) of green plant material, 1% (1%) seed fragments, and

61% (100%) unidentified (Clark, 1973). The fungus *Endogone* occurred in 27 to 31% of the stomachs of voles ($n = 28$) in Colorado (Williams and Finney, 1964). Bark and leaves of sagebrush were consumed in winter in Nevada (Linsdale, 1938).

Densities differ because of habitat quality (Brown, 1967; Van Horne, 1982), seasonal recruitment (Van Horne, 1982), and possibly as a result of multiannual fluctuations (Randall and Johnson, 1979) as commonly observed in other microtines. Wyoming populations had higher densities in willow-alder, aspen, and in subalpine meadows (Brown, 1967). Van Horne (1982) observed that clear-cuttings from 7 to 10 years of age that contained open areas, and shrub and sapling cover, are near optimum for *M. longicaudus* in Alaska. Highest densities were related to high productivity in the herbaceous and shrub flora. Densities were lower in habitats with thicker canopies and less ground herbaceous and shrub cover in later seral stages of the community (Van Horne, 1982). Peak densities occurred in late August to early September in Alaska, and were related to recruitment (Van Horne, 1982).

The minimum density was 4.9/ha in California populations, and rose to a maximum of 16.0/ha (Jenkins, 1948). Van Horne (1982) observed that 10 to 14 animals/ha was typical for Alaskan populations, and 53/ha was the maximum. Fluctuations from 20 to 120 voles/ha were observed in New Mexico (Conley, 1976).

Long-tailed voles are caught in association with *Sorex vagrans*, *S. monticolus*, *S. cinereus*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Zapus princeps* through parts of its range (Armstrong, 1977; Brown, 1967; Feldhamer, 1979; Hoffmeister, 1956). *Microtus pennsylvanicus*, *Zapus hudsonius*, and *Clethrionomys gapperi* are associated with long-tailed voles in riparian habitats of the Black Hills of Wyoming and South Dakota (Turner, 1974). *Microtus richardsoni* commonly is collected with *M. longicaudus* in Wyoming (Negus, 1950; Negus and Findley, 1959). In eastern Oregon, *Perognathus parvus* is a common associate (Feldhamer, 1979). *M. longicaudus* can be found with *M. montanus* (Brown, 1967), although long-tailed voles may be physically displaced (Randall and Johnson, 1979), avoid encounters (D. V. Colvin, 1973), or be poor competitors (Halvorson, 1982).

Known endoparasites of *M. longicaudus* are limited to a protozoan, *Giardia* sp. (Wallis et al., 1984) and three species of nematodes, *Heligmosomoides longispiculatus* (Rausch, 1952), *H. microti* (Kinsella, 1967), and *H. montanus* (Durette-Desset, 1968). Ectoparasites are both numerous and diverse, and include five species of mites, *Androaelops fahrenheitzi*, *Eulaelaps stabularis*, *Haemogamasus occidentalis*, *H. reidi*, and *Laelaps kochi* (Whitaker and Maser, 1984); the flea, *Eptedia wenmanni* (Easton, 1982); the louse, *Hoplopleura acanthopus* (Hansen, 1964; Emerson et al., 1984), and two species of ticks, *Dermacentor andersoni* (Clark et al., 1970) and *Ixodes (Phleixodes) eastoni* (= *I. ochotonae-angustus* complex; Turner, 1974; Keirans and Clifford, 1983).

Few predators have been documented to eat *M. longicaudus*. Barn owls (*Tyto alba*; Roth and Powers, 1979; Maser and Brodie, 1966), great horned owls (*Bubo virginianus*; Seidensticker, 1968; Maser and Brodie, 1966), long-eared owls (*Asio otus*; Maser and Brodie, 1966) and short-eared owls (*Asio flammeus*; Fitzner and Fitzner, 1975) have been reported to consume long-tailed voles, though in unknown quantities because of the similarity in the cranial and mandibular remains of *M. longicaudus* and *M. montanus*. The prairie falcons (*Falco mexicanus*) is the only hawk reported to feed on them (Marti and Braun, 1975). Ermines (*Mustela erminea*; Hayward, 1949; Van Horne, 1982), long-tailed weasels (*Mustela frenata*; Quick, 1951), and pine martens (*Martes americana*; Zielinski et al., 1983) were observed or suspected to prey on *M. longicaudus* regularly.

BEHAVIOR. *Microtus longicaudus* ordinarily does not construct well-defined runways (Hall, 1946; Howell, 1924). The greatest distance among multiple recapture sites was used as an index to size of home ranges of long-tailed voles in California (Jenkins, 1948). The average distance was 53 m; males had a larger home range length (59 m) than females (49 m). Furthermore, three males moved over 1,000 m. Home ranges of adult males were larger than those of adult females in populations in Alaska (Van Horne, 1982). Most observed activity was nocturnal, and no correlation of activity to weather conditions was observed (Van Horne, 1982).

Long-tailed voles apparently are capable of coexisting with other microtine species (Clark, 1973), however, *M. longicaudus* is timid (D. V. Colvin, 1973), thus they avoid encounters with other

species of *Microtus* (D. V. Colvin, 1973; Randall, 1978). When *M. longicaudus* is found with *M. montanus*, the more aggressive *M. montanus* (Randall, 1978) seems to displace long-tailed voles as their density increases (Randall and Johnson, 1979). Intraspecific aggression increases with the density of *M. longicaudus* (Conley, 1976).

Neonates produce ultrasonic sounds when disturbed or subjected to stressful conditions, and these calls attract the attention of the parents (M. A. Colvin, 1973).

GENETICS. Karyotypic variation has been observed for *M. longicaudus*. Individuals from Washington (Matthey, 1955), northern Oregon (Hsu and Benirschke, 1969), Arizona, Colorado, and New Mexico (Judd and Cross, 1980) have a diploid number of 56, of which 30 autosomes are metacentric or submetacentric and 24 are subtelocentric or acrocentric. The large number of biarms for the subfamily is believed to be the result of fusions and pericentric inversions (Matthey, 1957, 1973). The X chromosome is a large submetacentric and the Y chromosome is a small acrocentric. Six other cytotypes have been reported from southern Oregon and northern California ($2n = 57, 58, 59, 62, 66, \text{ and } 70$), and involve additions of supernumerary or B-chromosomes, and pericentric inversions (Judd and Cross, 1980).

An albino female was described from New Mexico (Fries et al., 1982).

REMARKS. The name *Microtus* is Greek *mikros* meaning small and *otus* meaning ear; *longicaudus* is from the Latin *longus* meaning long and *cauda* meaning tail. The authors wish to thank M. L. Johnson for supplying the photograph appearing in this account.

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