

Microtus montanus. By Wendy E. Sera and Cathleen N. Early

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***Microtus montanus* (Peale, 1848)**

Montane Vole

Arvicola montana Peale, 1848:44. Type locality “near to the head waters of the Sacramento River [= near Mt. Shasta, Siskiyou Co.], in California.”

Arvicola longirostris Baird, 1857 [1858]:530. Type locality “Upper Pit River, California.” This type locality is unlikely, considering the timing of the expedition (Kellogg 1922).

Arvicola nanus Merriam, 1891:63. Type locality “Pahsimeroi Mountains, Idaho (altitude 2,850 m or 9,350 feet)” = head of Pahsimeroi River, Custer Co..

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

Microtus dutcheri Bailey, 1898:85. Type locality “Big Cottonwood Meadows, near Mt. Whitney, Calif. (10,000 feet alt.)” Restricted to “southeast of Mt. Whitney, 10,100 feet altitude, Inyo Co., California” by Anderson (1959:472).

Microtus nevadensis Bailey, 1898:86. Type locality “Ash Meadows, Nye Co., Nevada.”

Microtus nanus Bailey, 1898:87. Type locality “Conconully [Okanogan Co.], Washington.”

CONTEXT AND CONTENT. Order Rodentia, superfamily Muroidea, family Muridae, subfamily Arvicolinae (Carleton and Musser 1984), genus *Microtus*, subgenus *Microtus* (Hall 1981). The subgenus contains 12 extant species in the Nearctic (Hall and Cockrum 1953). Hall (1981) recognized 15 subspecies of *M. montanus*. *M. m. amosus* is known only from the type locality and may be part of *M. m. rivularis* (Anderson 1959; Stock 1970).

M. m. amosus Hall and Hayward, 1941:105. Type locality “Torrey, Wayne County, Utah.”

M. m. arizonensis Bailey, 1898:88. Type locality “Springerville [Apache Co.], Arizona.”

M. m. canescens Bailey, 1898:87. Type locality “Conconully [Okanogan Co.], Washington.”

M. m. codiensis Anderson, 1954:497. Type locality “3 1/5 miles E and 3/5 miles S Cody, 5020 feet, Park Co., Wyoming.”

M. m. dutcheri Bailey, 1898:85, see above.

M. m. fucosus Hall, 1935:421. Type locality “Hiko, 4000 feet altitude, Pahrangat Valley, Lincoln County, Nevada.”

M. m. fuscus Hall, 1938:131. Type locality “2½ miles east of summit of Cochetopa Pass, Saguache County, Colorado.”

M. m. micropus Hall, 1935:417. Type locality “Cleveland Ranch, 6000 feet altitude, Spring Valley, White Pine County, Nevada.”

M. m. montanus (Peale, 1848:44), see above (*longirostris* Baird and *yosemite* Grinnell are synonyms).

M. m. nanus (Merriam, 1891:63), see above (*caryi* Bailey and *nexus* Hall and Hayward are synonyms).

M. m. nevadensis Bailey, 1898:86, see above.

M. m. pratincola Hall and Kelson, 1951:75. Type locality “6 miles E Hamilton, 3700 feet, Ravalli County, Montana.”

M. m. rivularis Bailey, 1898:87. Type locality “St. George [Washington County], Utah.” Known only from type locality (Anderson 1959).

M. m. undosus Hall, 1935:420. Type locality “Lovelock, Pershing County, Nevada.”

M. m. zygomaticus Anderson, 1954:500. Type locality “Medicine Wheel Ranch, 9000 feet, 28 miles E Lovell, Big Horn County, Wyoming.”

DIAGNOSIS. *Microtus montanus* (Fig. 1) is distinguished from *Arvicola richardsoni*, *M. californicus*, *M. canicaudus*, and *M. townsendii* by a combination of the following (Hall 1981; Verts

and Carraway 1998; Fig. 2): length of tail <50% of length of head and body, incise foramina ≤ 5 mm long and abruptly constricted posteriorly, incisors barely protruding beyond nasals in dorsal view, condylobasal length <35 mm, and length of hind foot >40% of tail length. *M. montanus* has 3 closed triangles on M3 and 8 mammae, whereas the potentially sympatric *M. ochrogaster* has only 2 closed triangles on M3 and 6 mammae. Upper body of sympatric *M. townsendii* has more dark brown or black with a heavier mixture of black-tipped guard hairs than *M. montanus*, which has a more buffy and grayish wash where these 2 species overlap (Hall 1981). *M. montanus* is distinguished from allopatric *M. canicaudus* (formerly considered a geographic race of *M. montanus*—Hall and Kelson 1951) by a distinctive karyotype (Hsu and Johnson 1970; Modi 1986) and different globulin- and hemoglobin-banding patterns (Johnson 1968). In addition, *M. canicaudus* has a more yellow upper body (Hall 1981).

GENERAL CHARACTERS. Upper body is some shade of brown, often with a buffy or gray wash, with a mixture of black-tipped hairs. Sides are paler and more buffy than upper body, and venter is white to gray, sometimes washed with buffy. Tail is bicolored, with blackish brown to black above and gray or white below (Hall 1981).

Darker pelage is more pronounced in southwestern part of range and is more diluted with paler hair or other colors of hair (including red, gray, or brown) to north and east (Anderson 1959). Grayest individuals are generally in northern part of range. Female pelage color varies more than does that of males (Howell 1924).

Ranges for standard external measurements (lengths in mm) are: total length, 140–220; length of tail, 24–69; length of hind foot, 14–27; mass, 37.3–85.0 g ($n = 4,722$ —Anderson 1959). *M. montanus* is a medium-sized vole, but body size can vary with sex, age, geographic location, or subspecies (Anderson 1959). Sexual dimorphism is slight. Generally, males are slightly more variable and on average slightly larger than females, but these trends are not significant (Anderson 1959; Howell 1924). Means \pm SD with ranges (in parentheses) of body dimensions (in mm) and mass (g) for 25 males and 41 females, respectively, from a single population (Howell 1924) are: length of head and body, 120.60 ± 9.29 (97–134), 117.51 ± 7.54 (93–130); length of tail, 47.92 ± 4.27 (38–55), 46.15 ± 2.78 (39–50); length of hind foot, 22.04 ± 0.75 (21–23), 21.52 ± 0.52 (20.5–22.5); and mass, 51.36 ± 11.27 (26.5–70.7), 47.35 ± 8.46 (22.9–62.2). Mean body mass of males from 9 populations was $47.9 \text{ g} \pm 3.7 \text{ SD}$, whereas mean body mass of females from 8 populations was $46.9 \pm 2.8 \text{ g}$ (Innes and Millar 1994).



FIG. 1. Photograph of an adult *Microtus montanus*. Photograph by David R. Rabon, Jr.

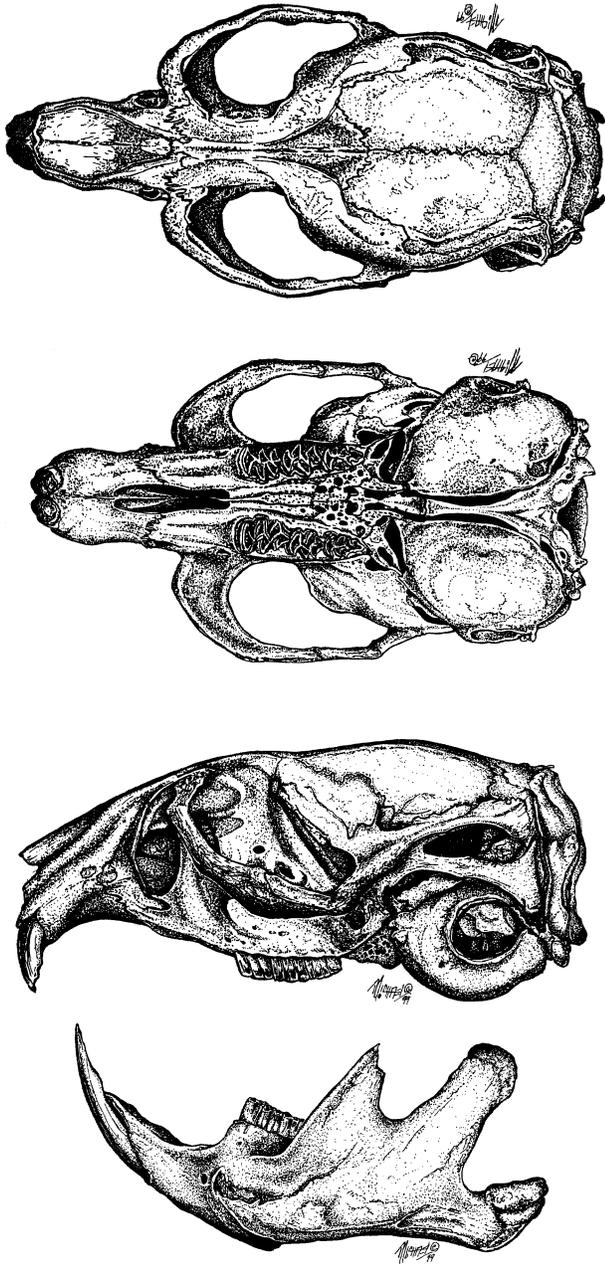


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Microtus montanus nanus*, from Mosquito Park Ranger Station, 2,897.5 m, 38.5 km W and 5.5 km N of Lander, Fremont County, Wyoming (Museum of Natural History, University of Kansas, No. 32803). Collected by Rollin H. Baker on 20 July 1949. Greatest length of cranium is 25.1 mm. Biological illustration by Michael A. Alford.

In general, montane voles are larger in areas that are warmer, more southern, and at lower altitudes, areas where interspecific competition from closely related species is lowest (Anderson 1959). Overall, largest individuals are in southwestern part of range and smallest in northern part (Anderson 1959). Mean hind foot length is shorter in eastern part of range than in western part, whereas tail length shows no geographic trends. Means and ranges of standard external body and cranial measurements by geographic location and subspecies are available (Anderson 1954, 1959).

DISTRIBUTION. Range of *M. montanus* is centered in montane and intermontane areas of the western United States from the Rocky Mountains, extending northward into south-central British Columbia, west to the eastern sides of the Cascade and Sierra Nevada ranges, south into the mountains of northern New Mexico,

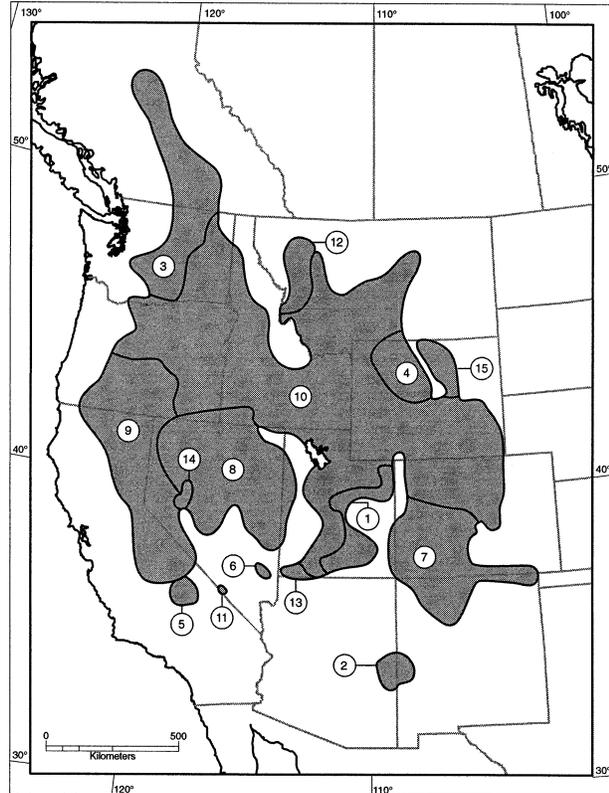


FIG. 3. Geographic distribution of *Microtus montanus* and its subspecies in western North America (modified from Dalquest 1975; Frey et al. 1995; Hall 1981): 1) *M. m. amosus*, 2) *M. m. arizonensis*, 3) *M. m. canescens*, 4) *M. m. codiensis*, 5) *M. m. dutcheri*, 6) *M. m. fucosus*, 7) *M. m. fusus*, 8) *M. m. micropus*, 9) *M. m. montanus*, 10) *M. m. nanus*, 11) *M. m. nevadensis*, 12) *M. m. pratincola*, 13) *M. m. rivularis*, 14) *M. m. undosus*, and 15) *M. m. zygomaticus*.

and east along the length of the Colorado–New Mexico border (Fig. 3). The southernmost population is isolated in the White and Blue mountains of east-central Arizona and the adjacent mountains of west-central New Mexico (Frey et al. 1995; Hall 1981) and is recognized as a distinct subspecies, *M. m. arizonensis* (Anderson 1959; Frey 1994). Other subspecies from the southern limits of the distribution are known only from isolated populations.

Microtus montanus occurs at higher elevations in the southern part of its range than in the Great Basin and northern part of its range (Anderson 1959). In Colorado, *M. montanus* occurs from ca. 2,074 m to well above timberline (Armstrong et al. 1973), whereas in northern California, it occurs from 824 m to above timberline (Kellogg 1922). *M. montanus* is absent from lower elevations of the Great Basin, lower elevations west of the Sierra Nevada, and east of the Rockies (Anderson 1959; Findley 1954).

FOSSIL RECORD. The genus *Microtus* probably originated in Asia with the 1st migration to North America across the Bering land bridge 1.8 million years ago (Zakrzewski 1985). *M. montanus* possesses 1 of the most derived karyotypes among the New World *Microtus*; thus, it probably has had a long, independent history in the New World (Hoffmann and Koepl 1985). The origin of *M. montanus* is suspected to be from the *M. paroperarius* (early Pleistocene, ca. 1.4 million years ago)–*M. pennsylvanicus* (mid-Pleistocene, ca. 0.6 million years ago) lineage, but may be derived from another New World lineage (Hoffmann and Koepl 1985; Zakrzewski 1985).

Fossils of *M. montanus* occur from >24 sites in 10 states (Arizona, Colorado, Idaho, Kansas, Nevada, New Mexico, Oregon, Texas, Utah, and Wyoming) and Alberta, Canada, ranging in age from Irvingtonian (Kansan or ca. 1.2 million years ago) to Holocene (ca. 10,000 years ago—Zakrzewski 1985). Earliest fossil records are from Idaho and Utah. Fossil remains of *M. montanus* are dif-

difficult to distinguish from those of *M. longicaudus* because of the similarity in dental and cranial morphologies. Sites in Kansas, Texas, New Mexico, Nevada (if not *M. californicus*), and Alberta (if not *M. longicaudus*) are outside the present range of *M. montanus* (Zakrzewski 1985). Other fossil sites include Porcupine Cave in Colorado (Barnosky and Bell 1994), Nebraska (Voorhies and Corner 1985), Snake Creek Burial Cave in Nevada (Bell and Mead 1998), and Crystal Ball Cave in Utah (Heaton 1985).

The fact that *M. montanus* occurs in isolated populations in southwestern United States suggests that favorable habitats were once continuous over the entire area (Findley and Jones 1962). The montane vole may have been widespread across the Southwest during the height of the Wisconsinan glaciation (a cool, moist period) and occurred in large, continuous populations across its entire range (Findley and Jones 1962). Subsequently, as aridity increased, the montane vole retreated to mesic refugia, and its distribution became progressively restricted and fragmented. At the southern limits of its range, *M. montanus* is now primarily restricted to mesic, high-elevation habitats (Anderson 1959; Dalquest 1975; Findley and Jones 1962). Similar isolations may account for the current discontinuous distribution of the montane vole over much of its range (Anderson 1959; Hoffmann and Koepl 1985).

FORM. Changes in external measurements occur with increasing age, making separation of body size variation due to age from other sources of variation, especially geographic, difficult. Young may be produced throughout the year, and age classes are not easily distinguishable primarily because montane voles continue to grow into adulthood and possibly throughout life (Anderson 1959). In addition, common landmarks used to assign age class in other species, such as eruption of particular teeth, appearance of wear on certain cusps, or fusion of certain skull sutures, are not useful in *M. montanus* because teeth grow continuously, most adults lack enamel crowned cusps, and skull continues to grow throughout adulthood. Sexual maturity is not a useful criterion for age because individuals may breed when only half their adult weight (Anderson 1959).

Dental formula of *M. montanus* is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Fig. 2). Descriptions of dentition, including the extensive molar variation in the patterns of the 1st lower and 3rd upper molars, as well as descriptions and figures of cranial and mandible morphology, including bone structure and musculature, are available (Howell 1924).

Six plantar tubercles are usual (Hall 1981), but these vary in size and number, even within a single population (Howell 1924). The 4 pairs of mammae include 2 pectoral and 2 inguinal (Howell 1924). Montane voles have vesicular, preputial, anal, and hip glands, all of which hypertrophy in response to testosterone and become more pronounced at puberty in males (Jannett 1978a). Within a single population, hip glands were absent in juveniles, larger in older females than in subadult males, and largest in adult males (Howell 1924). Preputial glands of *M. montanus* are much larger than those of the sympatric *M. pennsylvanicus* and contain species-typical fatty acid esters of short-chain alcohols (Welsh et al. 1988). These esters may function as species-specific recognition cues where these 2 species are sympatric. Montane voles have a mean of 3.3 Meibomian glands (range, 2–4; $n = 3$ individuals) in each dorsal eyelid and 0.3 (range, 0–1; $n = 3$) in each ventral eyelid, which, in both cases, is slightly below average for a microtine (Quay 1954).

Bacular stalk is broad; greatest length varies from 2.3 to 3.1 mm, 1.5 to 1.75 times the greatest breadth and 3.33 to 4.33 times the greatest depth, depending on subspecies (Anderson 1960). Base is broad and wider ventrally than dorsally. Of the 3 ossified processes, the median process is largest and is more than twice as wide as deep, laterally compressed distally, and one-third to two-fifths the length of the stalk; lateral processes are shorter and more slender. Bacular shaft is relatively slender, terminally rounded, slightly inflated, slightly wider than high at the midpoint, and one-fourth as wide as the base of the stalk. Ontogenetic development of baculum of *M. montanus* from neonates to adults has been described (Arata et al. 1965).

Dorsal lobe of glans penis is double-peaked and nonpapillose (Hooper and Hart 1962). Papillae on ventrolateral sectors are variable in size, shape, and number but tend to be short with 3 to 6 distinct fingers per sector. Urethral process has curved lateral lobes that are often asymmetrical, each with a large accessory tubercle.

Medial lobe is as long as lateral lobes, and in 2 of the 3 specimens, it was split distally. Average measurements from 3 specimens were: length, 4.6 mm and diameter, 2.8 mm (no range given—Hooper and Hart 1962). Female montane voles lack a baubellum (os clitoris), but the clitoris has 3 cartilaginous lobes (Arata et al. 1965).

FUNCTION. Standard metabolic rate of cold-acclimated montane voles averaged 2.65 cc O₂ g⁻¹ h⁻¹ (no range given; $n = 10$ —Packard 1968). The thermoneutral zone of cold-acclimated animals is 26 to 31°C (Packard 1968). Below 26°C, oxygen consumption is an inverse linear function of ambient temperature. Minimal thermal conductance is ca. 0.816 cal g⁻¹ h⁻¹ °C⁻¹ (no range given; $n = 10$). Body temperature is independent of ambient temperature between -5°C and 26°C, and average 37.5–37.8°C (range, 36.0–38.5; $n = 10$). Montane voles die above ambient temperatures of 31°C.

Female montane voles deprived of light have lower body, ovary, uterus, adrenal, Harderian gland, and, to some extent, kidney weights (Vaughan et al. 1973). Montane voles born under long photoperiod completed juvenile and subadult molts and began the adult molt before animals born under short photoperiod (Pinter 1968). Both guard hairs and underfur of juveniles and subadults are longer under short photoperiods.

Male montane voles lack the anteroventral–periventricular nucleus and have a larger sexually dimorphic nucleus of the preoptic area volume than females (Shapiro et al. 1991). *M. montanus* differs from *M. ochrogaster* in the neural distribution of oxytocin and vasopressin receptors (Wang et al. 1996). Differences in receptor binding were evident in the lateral septum of neonates and reached adult levels at weaning (3 weeks of age—Wang and Young 1997). Male montane voles have a higher density of vasopressin immunoreactivity projections to the lateral septum and lateral habenular nucleus than females (Wang et al. 1996).

ONTOGENY AND REPRODUCTION. Breeding for *M. montanus* begins in April or May, after the spring snowmelt, and continues through August (Negus et al. 1992) or through September or November (Vaughan 1969). However, in an increasing population of montane voles in northwestern Wyoming, females of all ages displayed subnivean midwinter reproduction (Jannett 1984). From 39% to 68% of the potentially breeding females bred during the winter, including both primiparous and multiparous females. The chemical, 6-methoxybenzoxazolinone (6-MBOA), which voles ingest when they eat new spring grass, triggers the reproductive effort (Berger et al. 1981; Sanders et al. 1981). Cinnamic acids and related vinyl phenols found in mature and senescent grasses typical of late summer depress reproduction (Berger et al. 1977). Dietary supplements of these compounds result in decreased uterine weight, inhibition of follicular development, and decreased reproductive activity.

Microtus montanus females do not exhibit regular estrus cycles, either when isolated or when exposed to males in the laboratory (Gray et al. 1974); in contrast, some female montane voles may cycle in the presence of males (Shapiro and Dewsbury 1990). *M. montanus* has a postpartum estrus (Gray et al. 1974; Vaughan et al. 1973). Ovulation is induced by contact with males, especially if copulation takes place (Gray et al. 1974), and increasing amounts of copulatory stimulation increase the probability of ovulation (Davis et al. 1974). A critical number of copulations are required to maintain the corpora lutea. Only 1 of 10 females had implanted embryos 8 days after copulations limited to a single ejaculatory series (Kenney and Dewsbury 1977). Females whose mate was removed within 24 h of 1st copulation were less likely to be pregnant 7 days later (30–66% pregnant versus 97–100% pregnant in the control group—Berger and Negus 1982). High levels of vaginal cornification are present in the vaginal smears of both nulliparous (79.3–83.3%) and parous (56.6–96.0%) females (Taylor et al. 1992). Brief exposure to males results in behavioral receptivity (Taylor et al. 1992). Female *M. montanus* often mate when 1st exposed to males (Taylor et al. 1992) and have no preference for previously mated or nonmated males (Pierce and Dewsbury 1991). Vaginal opening and vaginal smears dominated by cornified cells occurred earlier in females that had direct contact with males than in those females separated from males by a hardware cloth barrier (Sawrey and Dewsbury 1991). At least some females housed across a hardware cloth barrier from males showed signs of reproductive activation, indicating that chemical signals from males may play a

role in activating the female reproductive system (Sawrey and Dewsbury 1991). Postejaculatory intervals averaged ca. 6.5 min (no sample size or range given—Dewsbury 1973), and 5 additional thrusts delivered 15 min after an ejaculation reduced the number of sperm reaching the uterus by 70% (Dewsbury et al. 1992).

Gestation is 21 days, and average litter size is 6 pups in the laboratory (range, 3–9; $n = 42$ —Colvin and Colvin 1970; range, 5–8; $n = 8$ —McGuire and Novak 1986) and 5.8 pups \pm 0.25 SE in the field (embryo counts, range, 2–10; $n = 46$ —Hoffmann 1958; Vaughan 1969). Average litter size varies with female parity and age of 1st reproduction (Negus and Pinter 1965). Litter size increases with parity through the 5th litter, after which litter size decreases. Average litter size for the 1st litter for females that began breeding as subadults was 3.6 pups (range, 1–5; $n = 31$) in contrast to 4.2 (range, 2–6; $n = 12$) for females that were adults when their 1st litter was produced (Negus and Pinter 1965). Exposure to an unfamiliar male at midgestation may induce abortion, especially if the female is nulliparous (Stehn and Jannett 1981). Preimplantation mortality ranges from 4.9% to 12.6% ($n = 106$), and postimplantation mortality ranges from 2.6% to 3.9% ($n = 94$ —Hoffmann 1958).

Neonates are born hairless and toothless, with eyes and ears closed and toes fused. Pinna becomes detached on day 3, incisors erupt at 3–5 days, fur is visible at 4–5 days, eyes open around 10 days, and toes separate at 10–12 days (Shapiro and Insel 1990; Siedel and Booth 1960). Pups can right themselves at 4 days, leave the nest at ca. 10–13 days, and begin to consume solid food by the 13th day, with the last observed nipple attachment by the 14th day (McGuire and Novak 1986; Shapiro and Insel 1990). Growth rate in *M. montanus* is ca. 0.63 g/day (Wunder 1985), but growth rates vary with age and season of birth (Siedel and Booth 1960). Growth rates of pups and subadults are reduced under a short photoperiod of 6:18 relative to growth rates under a long photoperiod of 18:6 (Petterborg 1978). Except in high-density populations, females abandon the natal nest when pups are around 15 days old and prepare a new nest for the next litter (Jannett 1978b; McGuire and Novak 1986).

In a predictable marsh environment in Utah, 3–4 cohorts were produced each year, and each cohort has unique life-history characteristics (Negus et al. 1986). The 1st cohort, typically born in May, grows rapidly and is sexually mature at 4–5 weeks of age. These animals live ca. 6 months. The 2nd cohort matures at 7–8 weeks and lives ca. 7 months. The 3rd cohort overwinters and is not sexually mature until the next spring, at 28–30 weeks of age. They typically live ca. 12 months. The 4th cohort is numerically the smallest, and its members often fail to survive the winter. Montane voles exhibited a similar pattern in northwestern Wyoming during a year of normal rainfall. However, during a drought the following year, cohorts 1 and 2 did not reach sexual maturity during their birth year, and cohort 3 accounted for only 25% of total breeding recruitment, in contrast to over 70% the year before (Negus et al. 1992). In Colorado, all animals trapped by September were born that summer (Vaughan 1969).

Onset of sexual maturity is rapid for males raised under a longer photoperiod than that of their mother during gestation (Horton 1984). Males and females have higher growth rates when raised under longer photoperiod than the gestational photoperiod, and this effect results from factors working in utero, not during lactation (Horton 1985). Weight of reproductive organs (seminal vesicles or uterus) increases in response to maternal dosage of 6-MBOA during gestation (Berger et al. 1992). Offspring exposed to 6-MBOA during both gestation and lactation have increased gonadal size compared with unexposed offspring or those only exposed during either gestation or lactation (Frandsen et al. 1993). Number of litters produced increases and litter sex ratio is skewed toward females when breeding females are administered 6-MBOA (Berger et al. 1987).

Sexual maturity in females is accelerated by exposure to unfamiliar males (Sawrey and Dewsbury 1991). When young females (19 days old) are housed with a familiar male (either the biological father or foster father with whom she was raised) sexual maturity is not accelerated (Berger et al. 1997). Sexual maturity is induced by the biological father if he is unfamiliar to the female.

ECOLOGY. The geographic range of *M. montanus* overlaps that of *A. richardsoni*, *M. californicus*, *M. longicaudus*, *M. mexicanus*, *M. ochrogaster*, *M. oregoni*, *M. pennsylvanicus*, and *M. townsendii* (Anderson 1959). *M. californicus* on the western edge

of the range (Hoffmann 1958) and *M. ochrogaster* in central Montana (Hoffmann et al. 1969) are separated altitudinally from *M. montanus*, with the montane vole occurring at higher elevations. Where the ranges of *A. richardsoni* and *M. montanus* overlap in northwestern Wyoming and in Utah, *M. montanus* occurs at lower elevations, below the pine forests, in grassy meadows (Anderson 1959). In the White Mountains of Arizona, *M. mexicanus* occurs in drier, open, bunchgrass meadows, in contrast to *M. montanus*, which is restricted to mesic, grass-sedge meadows (Findley and Jones 1962).

In the Rocky Mountains of the western United States, *M. pennsylvanicus* is found in more mesic habitats and *M. montanus* is restricted to more xeric habitats, although home ranges of the 2 species may overlap (Hodgson 1972; Koplin and Hoffmann 1968; Stoecker 1972). Experimental removal of either species from an area of preferred habitat, where ranges overlap, resulted in the previously absent species moving into the newly vacated area (Koplin and Hoffmann 1968; Stoecker 1972). In experimental habitat chambers, *M. montanus* excludes *M. pennsylvanicus* through agnostic behavior, although frequently the 2 species remain separate through mutual avoidance (Stoecker 1972). However, *M. pennsylvanicus* dominates *M. montanus* in staged encounters. In field enclosures, individual home-range size increased for both species when they shared an enclosure compared with when 1 species occupied the enclosure (Douglass 1976). The increase for *M. montanus* was much greater than that for *M. pennsylvanicus* (224.4% of control compared with 117.8% of control—Douglass 1976).

In northeastern Nevada (Borell and Ellis 1934) and Colorado (Williams 1955), *M. montanus* occurs in drier areas, whereas *M. longicaudus* occupies wetter habitats. Generally, *M. montanus* is more abundant in grassy areas with more ground cover than the shrubby areas to which *M. longicaudus* is restricted (Clark 1973; Randall 1978). Strong interspecific aggression was not observed (Randall 1978).

Microtus montanus is sympatric with *Clethrionomys gapperi*, *Peromyscus maniculatus*, *Phenacomys intermedius*, and *Zapus princeps* over much of its range. *M. montanus* was most abundant in open canopy areas with dense vegetation (Belk et al. 1988). Although *C. gapperi*, *P. maniculatus*, and *Z. princeps* were captured on the same grids, *Z. princeps* was most likely to share the same microhabitat with *M. montanus*. Other sympatric rodents include *Dipodomys ordii* in southeastern Idaho (Koehler and Anderson 1991); *Lemmys curtatus* in Oregon (Maser et al. 1971) and Nevada (Borell and Ellis 1934); *Perognathus parvus* in Oregon (Feldhamer 1979); *Reithrodontomys megalotis* in Oregon (Feldhamer 1979), Utah (Egoscue 1961), and Nevada (Borell and Ellis 1934); and *Thomomys talpoides* in Montana (Grant et al. 1982). *Sorex vagrans* is frequently found with *M. montanus* in marshy areas (Borell and Ellis 1934; Feldhamer 1979). *S. cinereus* and *S. obscurus* occur in lower stream bottoms with *M. montanus* in Colorado (Williams 1955). In Colorado, *S. cinereus*, *S. merriami*, *S. nanus*, and *S. vagrans* occur at the same altitudes as *M. montanus* (Armstrong et al. 1973).

Microtus montanus occurs in communities ranging from grass- and sedge-dominated meadows to aspen or sagebrush, but the greatest abundance of montane voles is in areas with the most herbaceous cover (Clark 1973). Grass is the essential factor that characterizes *M. montanus* habitat, and this may partly explain the geographic differences in its altitudinal distribution (Anderson 1959; Findley 1954). Montane voles are restricted to grassy montane areas in the southern parts of its range but occur in both montane and grassy intermontane areas that characterize the northern parts of its range. Montane voles avoided areas denuded of vegetation by pocket gopher activity (Vaughan 1974), but during winter, montane voles were active under snow in areas too dry and open to be used during summer (Borell and Ellis 1934). Animals experimentally raised in shrubby habitat prefer grassy habitat as adults (Randall 1978). Montane voles may be found in areas dominated by a single grass species or mixed herbaceous communities. Where a single grass dominates, that grass is the principle component of the diet (crested wheatgrass, *Agropyron cristatum*—Koehler and Anderson 1991; salt grass, *Distichlis stricta*—Negus et al. 1986).

Plant matter is always the largest fraction in the diet. Stomach contents of 139 montane voles from all plant communities in Grand Teton National Park, Wyoming, contained 63% green plant materials by volume, 25% hair, 8% seed fragments, 4% parasitic round-

worms, and trace amounts of arthropods (Clark 1973). In Colorado, leaves and forbs accounted for 85% of the diet and grasses only 9% ($n = 55$ stomachs—Vaughan 1974). The 2 most frequent forbs in the diet were consumed in proportions greater than their frequency in the habitat: *Vicia americana* accounted for 0.9% of plants available but 19.2% of the diet, and *Oenothera minor* accounted for 0.5% of plants available but 6.7% of the diet. Fungus made up 10% of the diet at the beginning of summer, before forbs were fully leafed out, but was not eaten at all during the rest of the summer (Vaughan 1974).

Microtus montanus may be prey to any small- or medium-sized predators in its habitat. Raptor predators include burrowing owls (*Speotyto cunicularia*), great horned owls (*Bubo virginianus*), kestrels (*Falco sparverius*), long-eared owls (*Asio otus*), marsh hawks (*Circus cyaneus*), rough-legged hawks (*Buteo lagopus*), and short-eared owls (*Asio flammeus*). In Idaho, *M. montanus* accounted for 28–80% of prey taken by great horned owls near agricultural sites ($n = 14$ nesting areas—Marti and Kochert 1996). In Oregon, 37.8% of great horned owl prey items were *M. montanus* ($n = 42$ pellets—Brodie and Maser 1967). Most *M. montanus* taken by short-eared owls in Montana were 20–30 g ($n = 273$ pellets), a typical body mass of subadults (Blem et al. 1993). In central Oregon, *M. montanus* composed 9.3% of the diets of great horned ($n = 9$ collections), long-eared ($n = 2$ collections), and short-eared ($n = 6$ collections) owls and were the 3rd, 4th, and 5th most common prey species taken by each owl species, respectively (Maser et al. 1970). In Oregon, *M. montanus* was a minor component of burrowing owl diet (4.6% by mass, 0.03% by item, $n = 5,559$ pellets from 65 nests—Green et al. 1993; 0.008% by item, $n = 347$ pellets—Maser et al. 1971). In a salt grass marsh in Utah, *M. montanus* was prey to coyotes (*Canis latrans*), kestrels, marsh hawks, rough-legged hawks, and short-eared owls (Negus et al. 1986). Two weasel species, *Mustela erminea* and *M. frenata*, rely heavily on the montane vole as a winter food source in the Sierra Nevada, California (Fitzgerald 1977).

Parasites include species of 23 mites, 5–6 ticks, 4 lice, 30 fleas, 5 cestodes, 2 nematodes, and 1 trematode (Timm 1985). Montane voles captured in Grand Teton National Park in Wyoming were infected with the following microbial endoparasites: *Entamoeba*, *Giardia*, *Spiroplasma* (Pinter et al. 1988), *Babesia microti*, *Grahamella*, *Hepatozoon*, and *Trypanosoma* (Watkins et al. 1991). In this population, the parasitic protozoan *B. microti*, which reproduces in erythrocytes, was most likely transmitted by the tick, *Ixodes eastoni* (Watkins et al. 1991). Of 257 *M. montanus* examined, 103 were infected with *B. microti*. Infected animals had significantly enlarged spleens and higher reticulocyte numbers; however, hematocrit values were not significantly different between infected and uninfected animals (Watkins et al. 1991). Seven of 63 *M. montanus* collected in northeastern California and Nevada carried hantavirus RNA (Otterson et al. 1996) that resembled the Prospect Hill virus found in *M. pennsylvanicus*. One of 33 montane voles from Yellowstone National Park carried antibodies reactive to Sin Nombre virus (Mills et al. 1998).

Microtus montanus is a model for African sleeping sickness caused by *Trypanosoma brucei gambiense* (Frommel et al. 1988, 1991; Seed and Hall 1980). *M. montanus* is easily infected with *T. b. gambiense* and exhibits many of the same symptoms seen in humans including lethargy (Frommel et al. 1988, 1991; Seed and Khalili 1971).

Multinomial population cycles were documented in *M. montanus* from northwestern Wyoming. Cycle length varied from 3 to 4 years (Pinter 1986). Growth rates and age at 1st reproduction of *M. montanus* in montane habitat in Wyoming vary in response to environmental conditions and result in unstable population age distributions and fluctuating densities (Negus et al. 1992). Largest litter sizes were associated with the increase phase of the cycle and smallest with the decline phase. Spring precipitation may drive litter size and population cycling for *M. montanus* living in areas with unpredictable environments such as montane habitats (Pinter 1988). *M. montanus* populations in a Utah salt marsh, a more predictable environment, did not cycle (Negus et al. 1986). In this predictable habitat, cohort production was uniform each year and densities were high (Negus et al. 1986). *M. montanus* populations can expand quickly when inhabiting unharvested forage crops (Getz 1985).

Sherman live traps baited with peanut butter and rolled oats or museum specials baited with peanut butter are used to census

populations of *M. montanus*. Apples and fudge may be mixed with peanut butter as bait (Jannett 1980). Longworth traps are also used (Sullivan et al. 1998). Providing bedding in live traps reduces trap mortality on cold nights. Irradiated wires implanted subcutaneously were used to follow movements and map home ranges (Jannett 1980). Toe clipping and ear tags are the most common methods of identification.

Determination of age class in the field is based on body mass, pelage, and sexual maturity. Eye lens mass versus age regressions for 1st through 4th generation captive animals are available (Gourley and Jannett 1975). Cranial mass versus body mass regressions allow classification by age from material recovered from owl pellets (Blem et al. 1993).

Captive montane voles are housed in polycarbonate cages or aquaria with hardware cloth lids and cedar chips, pine shavings, sawdust, or peat mixed with wood shavings as bedding. Often, cotton batting is added for nesting material. A layer of hay (McGuire and Novak 1986) placed on top of the bedding material provides structure and cover. Most montane voles are maintained on commercial rabbit chow (Berger et al. 1997; Dewsbury et al. 1992; Gourley and Jannett 1975).

Microtus montanus can have great economic impact on apple orchards. *M. montanus* reduced the production of apples in 1 orchard of 200 trees by 36% during a year of high vole density (Askham 1988). Various poisons are used to control vole populations in orchards. The use of chlorophacinone to kill voles should have little effect on raptors that may rely on the voles as prey because as much as 90% of the chlorophacinone ingested was broken down by the time the vole died (Askham and Poché 1992). Providing alternative food sources for voles in orchards during the winter may reduce the amount of bark damage to trees both above and below ground (Sullivan and Sullivan 1988). Herbicides that limit grassy cover in orchards reduce suitable habitat (Sullivan et al. 1998). Predator odors (e.g., *Mustela erminea*) also will reduce feeding damage (Sullivan et al. 1988, 1990).

BEHAVIOR. Montane voles are semifossorial and construct nests of grass above and below ground (Jannett 1978b, 1982). Brood nests, which are always below ground, are globular with a diameter of ca. 13 cm (Jannett 1982). Males may use gopher burrows in addition to burrows they dig themselves (Jannett 1982). Captive males and females do not differ in nest-building behavior (Hartung and Dewsbury 1979b). Most nests (48%) are cup-shaped, although platform and covered nests represent 24% and 22% of the nest types, respectively (Hartung and Dewsbury 1979b). In southeastern Idaho, average depth of montane vole burrows ranged from 21.1 cm \pm 6.6 SD ($n = 42$) to 23 \pm 10 cm ($n = 14$), and average length ranged from 100 \pm 60 cm ($n = 42$) to 133 \pm 82 cm ($n = 14$)—Laundré and Reynolds 1993; Reynolds and Wakkinen 1987; average maximum depth increased in sandier soils (Laundré and Reynolds 1993).

Males and parous females are intrasexually territorial (Jannett 1980). Males mark territory with urine and piles of feces left in conspicuous places in the runway system and engage in anal dragging and scooting, 2 activities that deposit gland secretions on substrates (Jannett 1981c). Males also mark tunnels by raising their hindquarters so that the hip glands rub the upper walls (Jannett 1974). Intense male–male fighting occurs after the spring snow melt-off, when territories are established (Jannett 1981c). A single male territory may overlap >1 female territory (Jannett 1981c). In high-density populations, operational sex ratios were as high as 1:5 (scrotal males to parous females—Jannett 1980, 1981c). Only 1 male survives when >1 male is added to an enclosure with a parous female (Jannett 1980, 1981c; Shapiro and Dewsbury 1990). *M. montanus* are monogamous when densities are very low (Jannett 1980); however, adult males only associated with females during estrus and could not be induced to enter burrows of females at other times. Females mate preferentially with 1 of 2 males when presented with a choice; however, they spend more time alone than with either male (Webster et al. 1982). Females show no preference toward a male they have previously copulated with over a novel male, either in time spent in association or in number of copulations (Shapiro et al. 1986). Males do not discriminate between mated and unmated females in their choice of mating partner (Ferguson et al. 1986). When 1 male and 2 females are placed in an enclosure together, both females may enter estrus and the male will mate with both of them (Shapiro and Dewsbury 1990). Montane voles spent

7% of their time in physical contact with conspecifics (Shapiro and Dewsbury 1990). Social isolation does not elicit distress calls in montane vole pups (Shapiro and Insel 1990).

Microtus montanus males prefer conspecific females over *M. canicaudus* females unless they were cross-fostered to *M. canicaudus* parents, in which case they do not discriminate. Females do not discriminate between conspecific males and *M. canicaudus* males unless cross-fostered to *M. canicaudus*, in which case they prefer males of the foster species (McDonald and Forslund 1978).

Sexually naive montane voles of both sexes spend more time investigating male-soiled than female-soiled bedding, but only females prefer bedding soiled by the other sex when the comparison stimulus was clean bedding. Sexually experienced males spend more time near female-soiled bedding than clean bedding but do not differentiate between male-soiled and female-soiled bedding (Sawrey and Dewsbury 1994).

During some sexual encounters, males attempt to contact the female's head or nape and the female rears up and slaps at the male with her forepaws (Pierce et al. 1991). The male may slap back at her, which leads to a boxing match. Eventually, the female tolerates the male's advances and he sniffs her anogenital region. Copulation soon follows. In other mating sequences, females typically stand still as the male approaches, and lordosis in the female is barely detectable during mounting (Dewsbury 1973). Copulatory behavior consists of thrusting during intromission, multiple intromissions per ejaculation, and a mean of 5 ejaculations preceding satiety. Satiety is reached when the male fails to complete an ejaculatory series. Ejaculation can be attained by satiated males when exposed to novel females (Dewsbury 1973).

Maternal care includes nursing, brooding, grooming, and pup retrieval (McGuire and Novak 1986). Paternal care is unlikely in wild populations of *M. montanus* because males do not share nests with females during the breeding season (Jannett 1980, 1981c, 1982). Paternal care is observed in laboratory animals housed in small cages (Hartung and Dewsbury 1979a) but not when housing provides enough space for males and females to establish separate nests (McGuire and Novak 1986). Males tolerate pups they encounter in runways or those that wander into the male's nest (McGuire and Novak 1986).

When stressed, pups younger than 15 days produce ultrasonic vocalizations from 26 to 36 Hz (Shapiro and Insel 1990). Parents of either sex are more likely to locate a pup using auditory rather than olfactory cues (Colvin 1973b). Pups weakly attach to nipples and are easily dislodged as the mother leaves the nest (Salo et al. 1994). Play-fighting in montane vole pups more closely resembles precopulatory behavior than agnostic behavior (Pierce et al. 1991). Double captures in live traps indicate that juvenile males forage or disperse together in late summer or fall (Feldhamer 1977).

Females abandon the natal nest when pups are ca. 15 days old and begin constructing a new nest for their next litter (Jannett 1980, 1982; McGuire and Novak 1986). In high-density populations, females remained in the brood nest longer and did not drive off the young, leading to formation of extended maternal families (Jannett 1978b, 1980). When neighboring females were removed, females in extended maternal families abandoned their nests to establish new ones in the now open territory (Jannett 1978b). Reproduction may be suppressed in younger females of extended maternal families during high population densities (Jannett 1978b).

During agnostic encounters, male montane voles typically attack the rump and flanks of their target (Pellis et al. 1992). In dyadic encounters with male conspecifics, *M. montanus* males consistently target hip glands of their antagonist (Jannett 1981b). During an agonistic encounter in the field between a male *M. montanus* and a male *M. longicaudus*, vocalization, chase, retreat, attack, and wrestle behaviors occurred (Colvin 1973a). *M. montanus* is more aggressive than *M. californicus*, *M. longicaudus*, and *M. pennsylvanicus*; however, *M. ochrogaster* is more aggressive than *M. montanus* (Colvin 1973a).

Nonsocial behaviors include locomotor-exploratory movements, wall seeking, rearing at a wall, head grooming, freezing, digging, and swimming (Wolff 1985). Montane voles are not prone to jumping and have not been observed climbing. They can swim (Evans et al. 1978). Males and females are equally able to locate a spatial goal without local cues in the Morris swim task (Sawrey et al. 1994). They show no depth discrimination in a visual cliff test (Sloane et al. 1978).

Captive montane voles are predominantly nocturnal under

long photoperiods (summer) and predominantly diurnal under short photoperiods (winter—Rowsemitt 1991). Activity monitored in the field during summer and autumn in southeastern Washington indicated a shift toward more nocturnal activity under long photoperiods (Drabek 1994). In addition, montane voles have bimodal activity patterns during the day in the hottest part of the summer; they avoid the highest daytime temperatures (Drabek 1994). Castrated males show increased diurnal activity and decreased nocturnal activity, whereas males with testosterone implants showed the opposite result and an overall increase in activity levels (Rowsemitt 1986, 1989).

GENETICS. *Microtus montanus* has karyotypic variation (Judd et al. 1980). Karyotypes of montane voles from Arizona (Modi 1986), California (Matthey 1954), Oregon (Jefferson and Deschutes counties—Hsu and Johnson 1970), Utah (Schmid 1967; Modi 1986), Washington (Hsu and Johnson 1970), and Wyoming (Modi 1986) have $2n = 24$ (FN = 44). Autosomes in these populations are biarmed and include 7 pairs of large metacentrics and submetacentrics, 1 of which is especially large. One pair of medium-sized chromosomes has a highly unequal arm ratio, and 1 pair of the smallest 3 pairs of autosomes is distinctly smaller than the other 2 (Hsu and Johnson 1970). Nine of the 11 pairs of autosomes have a centromeric heterochromatin, and the X and Y chromosomes are completely heterochromatic (Modi 1986). Sex chromosomes are acrocentric. The X chromosome is small and acrocentric, and the Y chromosome is the smallest of the complement (Hsu and Johnson 1970).

Microtus montanus from an unknown locality had $2n = 22$ (de la Maza and Sawyer 1976). Populations from Arizona (*M. m. arizonensis*) and New Mexico (*M. m. fuscus*) have $2n = 24$ (FN = 44), whereas specimens from Oregon (Jackson and Klamath counties; *M. m. montanus*) have $2n = 22$ (FN = 40—Judd et al. 1980). In both forms, autosomes were biarmed and sex chromosomes were acrocentric. The 22-chromosome form lacked the smallest pair of metacentrics (pair 8). Constitutive heterochromatin (i.e., C-bands) also differed; however, G-banding patterns and nucleolar organizing regions were nearly identical.

A single successful litter between a male *M. m. montanus* and a female *M. c. californicus* was reported (Hatfield 1935). The pair produced a litter of 4, but only 1 pup survived to maturity.

Several melanistic individuals were described from Oregon (Jewett 1955). In another population in Oregon, 21 of the 74 animals caught in the field displayed pelage of various shades of yellow, primarily on nose, venter, dorsal areas of feet, and tail (Maser et al. 1969). Two specimens with very dilute color were reported from Wyoming (Owen and Shackelford 1942). A single male montane vole from Grand Teton National Park in Wyoming had bilaterally symmetrical white spotting without dilution of eye color (Pinter 1979). The rest of the pelage was diluted but retained the agouti pattern. The white spotting was an autosomal dominant trait (Pinter 1979). Heterozygotes were spotted; homozygotes were white with black eyes but apparently suffered from anemia and usually died in utero or shortly after birth. The few homozygotes that reached puberty were sterile.

Albinos have been reported from Colorado (Warren 1929) and Grand Teton National Park in Wyoming (Jannett 1981a). Three albinos out of 4,500 montane voles were trapped during a 7-year period (Jannett 1981a). The albinos were the only pelage variants caught. Albinism in *M. montanus* is inherited as an autosomal homozygous recessive.

The pink-eyed dilution is known for *M. montanus* (Pinter and Negus 1971). Dorsal coat color is a pinkish ivory hue, and eyes are pink; however, melanin is not entirely excluded from the fur. Pink-eyed dilution in *M. montanus* is inherited as a simple Mendelian recessive trait. The reproductive performance of the mutants did not differ significantly from that of wild-type animals (Pinter and Negus 1971). However, several mutants displayed a behavioral anomaly in which they carried their heads permanently tilted to one side, and their tails were abnormally short.

A hairless mutation also occurs in *M. montanus* (Pinter and McLean 1970). The condition is characterized by a total loss of juvenile pelage, followed by a temporary regrowth of a sparse, hypopigmented fur. Some animals developed the "rhino" condition, characterized by skin cysts that resulted in grotesquely wrinkled skin. Hairlessness in *M. montanus* is inherited as a simple Men-

delian recessive character. Animals with the condition did not breed readily, although they were fertile.

Three DNA probes for DNA fingerprints of *M. montanus* have been assessed (Cummings and Hallett 1991). The best results were obtained with the SNAP[®] probe (Molecular BioSystems, San Diego, California—Edman et al. 1988), although a “mouse” probe from a *Mus musculus* genomic library (Elliot 1986) and (CAC)₅, an artificially synthesized probe (Shäfer et al. 1988), also revealed individual-specific DNA fingerprints. The probe can assign paternity when maternity is known and provide a general measure of genetic similarity among individuals in a *M. montanus* population.

CONSERVATION STATUS. *Microtus m. arizonensis* was initially listed as endangered in New Mexico in 1979 (group 1: prospects of survival or recruitment in jeopardy—New Mexico State Game Commission Regulation [NMSGCR] 599) because of its limited distribution and small population size (Frey et al. 1995). The listing was reaffirmed in 1990 (NMSGCR 680). In Utah, *M. m. rivularis* is a species of special concern due to declining populations and its limited distribution; however, it was not listed as endangered or threatened for the state in 1999. Other isolated subspecies of *M. montanus* are undoubtedly rare and perhaps even threatened or endangered based on their limited distribution, but these populations have not been studied in any systematic way.

REMARKS. According to Bailey (1900), the original type specimen of *M. montanus* collected by Peale (1848) near Mt. Shasta in California was lost. However, the series of 57 specimens that Bailey (1900) examined from this type locality agrees with Peale's original description of the species.

The generic name *Microtus* is from the Greek words *mikros* meaning small and *ous* or *otos* meaning ear; the specific name *montanus* is from Latin, meaning montane or pertaining to mountain. Common names in the literature include Cochetopar vole, dwarf field mouse, dwarf meadow mouse, Montana vole, montane meadow mouse, montane vole, mountain field-mouse, mountain vole, Peale meadow mouse, Peale's meadow mouse, and Peale vole.

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Associate editors of this account were ELAINE ANDERSON and LUI MARINELLI. Editor was VIRGINIA HAYSSSEN.

W. E. SERA, BIOLOGY PROGRAM, DIVISION OF NATURAL AND HEALTH SCIENCES, SETON HILL UNIVERSITY, GREENSBURG, PENNSYLVANIA 15601-1599. C. N. EARLY, DEPARTMENT OF BIOLOGY, BAYLOR UNIVERSITY, WACO, TEXAS 76798-7388.