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Microtus oregoni.

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Microtus oregoni (Bachman, 1839)

Creeping Vole

Arvicola oregoni Bachman, 1839:60. Type locality Astoria, Clatsop Co., Oregon.
Microtus oregoni Miller, 1896:9; first use of name combination.
Microtus bairdii Merriam, 1897:74. Type locality Glacier Peak, 7,800 ft, Crater Lake, Klamath Co., Oregon.
Microtus serpens Merriam, 1897:75. Type locality Agassiz, British Columbia.
Microtus morosus Elliot, 1899:227. Type locality Boulder Lake, 5,000 ft, Olympic Mts., Clallam Co., Washington.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Arvicolinae, Genus *Microtus*, Subgenus *Microtus* (Carleton and Musser, 1984; Hall, 1981; Hooper and Hart, 1962). Four subspecies are recognized currently (Hall, 1981):

M. o. adocetus Merriam, 1908:145. Type locality 2 mi S South Yolla Bolly Mt., 7,500 ft, Tehama Co., California.
M. o. bairdii Merriam, 1897:74, see above.
M. o. oregoni (Bachman, 1839:60), see above (*cantwelli* Taylor and *morosus* Elliot are synonyms).
M. o. serpens Merriam, 1897:75, see above.

DIAGNOSIS. *Microtus oregoni* can be distinguished from sympatric and parapatric voles on the Pacific coast on the basis of tiny eyes (opening about 2 mm in diameter), unrooted molars, reentrant angles on lingual side of lower molars about equal in depth to those on labial side, and M3 with three loops of enamel on the lingual side (Fig. 1). Adult creeping voles are the only *Microtus* in the Pacific Northwest, except *M. richardsoni*, with five plantar tubercles on the hindfeet (Hall, 1981).

GENERAL CHARACTERS. The creeping vole is the smallest vole within its geographical range; the species averages about 140 mm in total length and about 19 g in body mass (Bailey, 1900; Hall, 1981). Feet are pentadactyl (but pollex reduced and without a claw), plantigrade, and moderately furred on sole to level of tubercles (Miller, 1896); tail is short, less than 30% of total length (Fig. 2); ears are short, scantily haired, and protude slightly from fur; there are eight mammae, two pairs pectoral and two pairs inguinal (Bailey, 1900; 1936). Flank glands are obscure or lacking (Bailey, 1900; Hall, 1981).

The fur is short and dense. The dorsum is sooty gray to dark brown or black, often with a mixture of yellowish hairs; the venter is dusky washed with buff or white; the tail is sooty or blackish, and slightly lighter below; and fur on the ears is black (Bailey, 1900; Hall, 1981; Ingles, 1965).

The skull is low and flat, and the rostrum is long and slender in relation to remainder of the skull (Miller, 1896). Incisive foramina are relatively short and wide (1 by 4 mm) and often constricted slightly posteriorly (Anderson, 1960; Ingles, 1965; Maser and Storm, 1970); their shape and size are not considered diagnostic (Maser and Storm, 1970). Zygomatic arches are relatively thin (Maser and Storm, 1970).

Molars are small; m3 has two or three closed triangles; M1 has five closed triangles; in M2 the anterior pair of triangles are usually confluent; and M3 has three transverse loops (Bailey, 1900; Hall, 1981).

DISTRIBUTION. The geographic range of *Microtus oregoni* (Fig. 3) extends from Port Moody, southern British Columbia, Canada, south to Mendocino City, California, and eastward in Washington to Lake Chelan, Mt. Aix, and Signal Peak, in Oregon to the N base of Three Sisters and Crater Lake, and in California to Beswick and South Yolla Bolly Mt. (Hall, 1981). Altitudinally, creeping voles range from sea level (Dalquest, 1948) to nearly 2,400 m (Merriam, 1897). Goertz (1964) and Maser and Storm (1970:Map 15) indicated that the species did not occur in the Willamette Valley, Oregon, but specimens on deposit in the Oregon State University, Department of Fisheries and Wildlife Mammal Collection were collected in a coppice on the valley floor.

Van der Meulen (1978) believed that *Microtus* first immigrated from Eurasia more than 1.2 m.y.b.p., but seemingly there are no Pleistocene records of *M. oregoni* (E. Anderson, in litt.).

FORM AND FUNCTION. External measurements of *Microtus oregoni* (in mm) provided by Hall (1981) are: total length, 129 to 154; tail length, 32 to 42; hindfoot length, 16 to 19; ear length, 9 to 10. With few exceptions, these extremes were not exceeded by measurements provided by Bailey (1900, 1936), Banfield (1974), Cowan and Guiguet (1956), and Ingles (1965). However, measurements provided by Maser and Storm (1970) and by Taylor (1920) deviate considerably; their combined extremes are: total length, 124 to 161; tail length, 32 to 52; hindfoot length, 16 to 21; ear length 9 to 14. Body mass ranges from 14.5 to 27.5 g (Maser and Storm, 1970).

Maxima and minima for selected skull dimensions (in mm) are: basal length, 20.9 to 23.4; length of nasals, 6.7 to 7.3; zygomatic breadth, 14.0 to 14.9; mastoid breadth, 11.0 to 12.6; alveolar length of the upper molar row, 5.5 to 6.1 (Bailey, 1900; Taylor, 1920).

The glans penis, relatively simple like those of all Arvicolinae, is about 3.2 mm long and 1.9 mm in diameter with a smooth-edged dorsal lobe forming a single peak and three or four spine-tipped projections on lateral sections of the rim (Hooper and Hart, 1962). *M. oregoni* was the only Arvicolinae studied by Hooper and Hart (1962), other than *M. longicaudus* and *M. miurus*, that possessed a phallus with a two-coned dorsal papilla having spines on its sides and tip and a lateral-curving bilobed urethral process. The baculum (Fig. 4), about 3.0 mm in length (Hooper and Hart, 1962), has a broad stalk about 2.2 mm long with an inflated tip and three well-developed ossified processes. The median process is about 40% of the length of the stalk, tapered terminally, and flattened obliquely on its proximate end; lateral processes are about 67% of the length of the median process (Anderson, 1960).

Microtus oregoni has a mean of 3.2 ($n = 4$, range 2 to 5) meibomian (tarsal) glands in the dorsal eyelid and 1.2 ($n = 4$, range 0 to 3) in the ventral eyelid (Quay, 1954). Because the length of the eyelid is reduced in *M. oregoni*, the size of the glands in relation to the size of the eyelids is greater than in non-fossorial voles; reduced eye size and increased secretory protection for the eye may be related to a fossorial mode of life in voles although enlargement of tarsal glands does not occur in other fossorial rodents (Quay, 1954).

The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Seemingly, aspects of the physiology of the creeping vole have been neglected.

ONTOGENY AND REPRODUCTION. Mating in *M. oregoni* may occur over a period of about 5 h and includes periods of "vigorous squeaking" for 10 to 15 min at intervals of about 30 min. Copulations occur near the beginning of vocal periods, last 2 to 3 s, and are repeated frequently (Cowan and Arsenault, 1954). The vulva may or may not close following copulation, but it closes during anestrus in winter. Implantation occurs significantly more frequently (49 of 78) in the right horn of the uterus (Cowan and Arsenault, 1954).

The mean length of the gestation period is 23 days 20 h with a range of 23 days 8 h to 24 days 12 h ($n = 4$), somewhat longer than for other species of *Microtus*. Evidence that lactation extends gestation is lacking (Cowan and Arsenault, 1954).

Mean litter size of wild-caught creeping voles in Oregon was

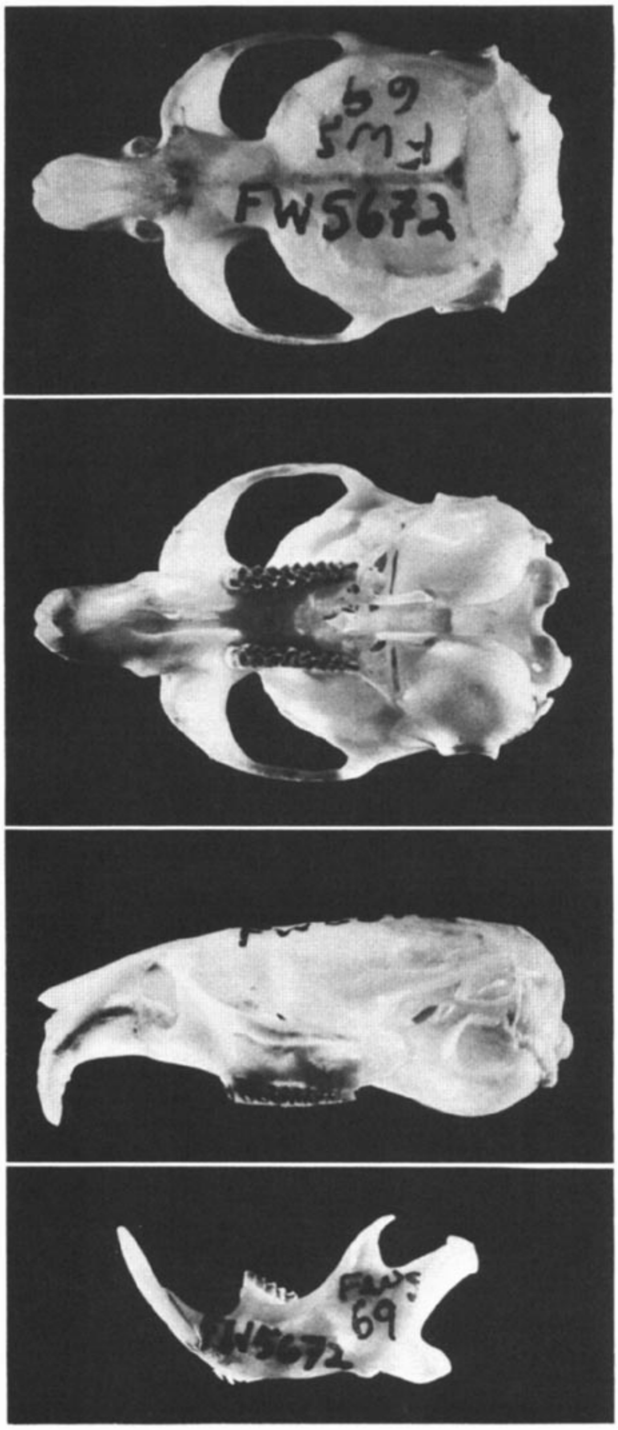

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Microtus oregoni* (OSUFW 5672 from Mary's Peak, 9 mi W, 2 mi S Philomath, Benton Co., Oregon, 4,000 ft). Occipitonasal length of skull is 23.1 mm.

3.4 based on counts of corpora lutea ($n = 34$), 3.1 based on counts of embryos ($n = 18$), and 3.5 based on counts of pigmented sites of implantation ($n = 11$); the combined mean was 3.2 (range 1 to 8). The 5% loss of potential offspring was attributed to resorption of embryos during gestation or disappearance of pigmented sites of implantation subsequently (Gashwiler, 1972). Hooven (1973) found a mean of 4.0 (range 1 to 8) embryos per pregnant female in a sample ($n = 21$) caught in Oregon. In British Columbia, mean litter size was 3.1 ($n = 26$; range 1 to 5) based on counts of embryos for wild-caught specimens and 2.8 ($n = 28$; range 1 to 5) for young born to captive females (Cowan and Arsenault, 1954). In a later study in British Columbia, a mean of 3.3 embryos per female ($n = 8$) was reported (Hawes, 1975). A mean of 3.8 young per litter (range 1 to 6) was born to captive females of Oregon stock maintained in Colorado (Colvin and Colvin, 1970). In captivity, mean litter size increases with successive litters at least through the first four litters; subsequent litters may be smaller (Cowan and Arsenault, 1954).

FIG. 2. Photograph of *Microtus oregoni* (OSUFW 7254). Note short tail and tiny eyes.

Cowan and Arsenault (1954) estimated that females produced a maximum of four or five litters annually; seemingly, the first three litters were produced with sufficient synchrony of breeding that three distinct age classes could be discerned among young caught April to June, but remaining litters were produced irregularly. Gashwiler (1972) estimated a mean of 4.8 litters per female annually in Oregon computed by a modification of a model suggested by Scheffer (1933).

The breeding season for creeping voles was considered to extend from March to September in Oregon and British Columbia (Cowan and Arsenault, 1954; Gashwiler, 1972), but a 30-day-old juvenile caught 6 December and another on 9 March, and the occurrence of fertile males in wild populations until 23 November, suggests that some individuals may breed both earlier and later. Cowan and Arsenault (1954) showed that breeding in a captive colony was stimulated by increasing the ambient temperature but not by altering the photoperiod, the latter likely because of the subterranean habits of creeping voles. To us, extension of the breeding season during mild winters seems possible.

At birth, creeping voles are pink, naked, with closed eyes, and with pinnae folded forward over the meatuses (Cowan and Arsenault, 1954). By 12 h after birth, the dorsum turns gray and downlike vibrissae appear; by 24 h, the dorsum is blackish and tips of soft hairs protrude; by 60 h, upper surfaces of legs and tail are dark and the pinnae begin to unfold; by 84 h, dorsal fur is colored, the incisors are visible beneath the gums, and the venter is sparsely furred; by 132 h, the young can crawl weakly and the incisors are erupted. The auditory meatuses are open by 10 days of age and the eyes open between 10 and 11.5 days; the molars erupt and the young begin to consume small amounts of green vegetation by 11.5 days; they can be weaned at 13 days (Cowan and Arsenault, 1954). Hooven (1973) reported that laboratory-raised young of Oregon stock opened their eyes at about 12 days and were weaned at about 15 days. Between 14 and 28 days, young do not attempt to avoid being touched as do adults.

In Oregon, body mass of newborn young presumably of litters born to females in traps averaged 1.6 g (Hooven, 1973). In a captive colony, body mass at birth averaged 1.7 g (range 1.6 to 2.2 g) with no significant differences between those in large and small litters (Cowan and Arsenault, 1954). Instantaneous growth rates (*K*) for these young ($n = 41$) for 0 to 9, 9 to 20, 20 to 30, and 30 to 38 days after birth in early summer were 0.162, 0.063, 0.033, 0.019, respectively; growth rates in late summer and winter were lower. Changes in growth rates that occurred 9 days after birth likely were in response to an inadequate supply of milk, whereas those that occurred at 20 days likely were in response to pubertal changes. Rates of gain in mass were similar for the sexes to 34 or 35 days, after which males gained faster. After attaining sexual

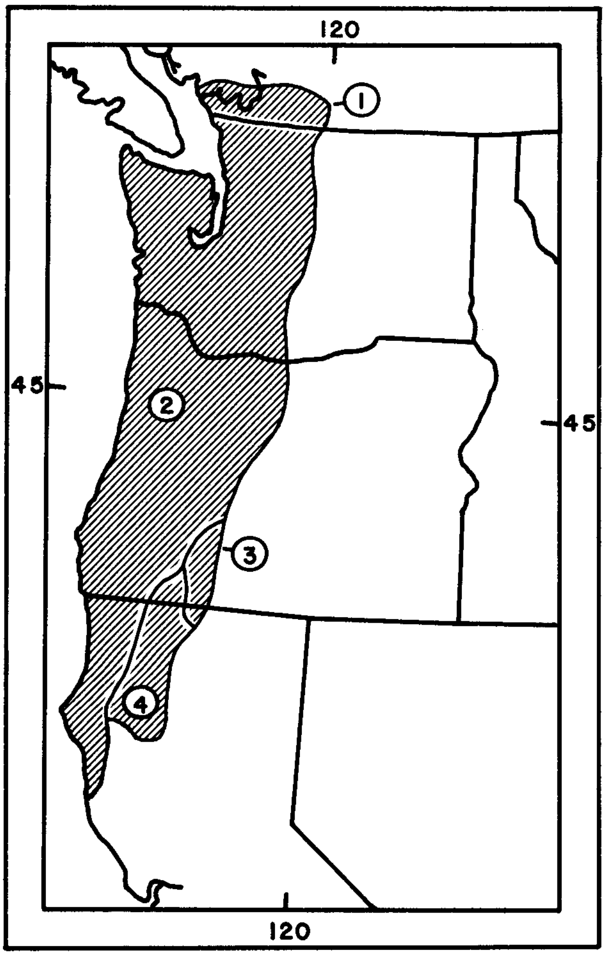

FIG. 3. Distribution of *Microtus oregoni*. Subspecies are: 1, *M. o. serpens*; 2, *M. o. oregoni*; 3, *M. o. bairdi*; 4, *M. o. adocetus*. Map modified from Hall (1981) and Hatfield and Hooper (1935).

maturity, body mass of males more or less stabilized until paired with a female, whereupon males gained 5 to 10 g that was maintained through the breeding season or until separated from the female (Cowan and Arsenault, 1954).

Cowan and Arsenault (1954) were unable to distinguish the sexes of *M. oregoni* with certainty before 22 to 26 days of age, although they thought that females might attain puberty before that age. Females born in early litters became breeders if they attained puberty before the last week of July; among these females, the first estrus occurred at 22 to 24 days, but all copulations before 27 days of age, and most before 35 to 36 days, did not result in pregnancy. These observations led to the suggestion that a period of sterility lasting 5 to 14 days followed puberty (Cowan and Arsenault, 1954). Males between 34 and 38 days of age copulated with experienced females with which they were paired, but were unable to inseminate them. Spermatozoa occurred in epididymides of 6-week-old males, but were not abundant until they were 7 to 8 weeks old.

Intervals between successive litters of 23.5 to 25 days among 7 of 11 females for which the interval was known indicate that female creeping voles have a postpartum estrus probably within 36 h of parturition (Cowan and Arsenault, 1954).

ECOLOGY. Creeping voles usually are considered components of communities composing all stages of the moist coniferous-forest sere (Dalquest, 1948; Gashwiler, 1972; Goertz, 1964). Cowan and Guiguet (1956:215) claimed the species was "confined to the deciduous forest region" in British Columbia, although subsequent ecological studies of *M. oregoni* were conducted in early stages of the coniferous forest sere in the region (Hawes, 1975; Sullivan, 1979, 1980). Clear-cuttings, especially those on which logging slash is burned, support 3 to 8 times more *M. oregoni* than stands of virgin forest (Gashwiler, 1972; Goertz, 1964; Hawes, 1975; Hooven and Black, 1976). Within these moist environments, creeping voles seem to be most abundant in more xeric sites, especially those supporting stands of short grass (Dalquest, 1948; Goertz, 1964; Hawes, 1975). Hooven (1973) suggested that creeping voles required ground cover or mulch, but that grass sods were avoided; nevertheless, he and coworkers showed that populations of *M. oregoni* were reduced or eliminated by applications of herbicides to selectively reduce grasses and forbs on clear-cuttings (Black and Hooven, 1974; Borrecco et al., 1979). Where grasses are absent or comprise only a small part of the vegetation, creeping voles are more abundant in herbaceous-dominated sites than where woody plants predominate (Gashwiler, 1970).

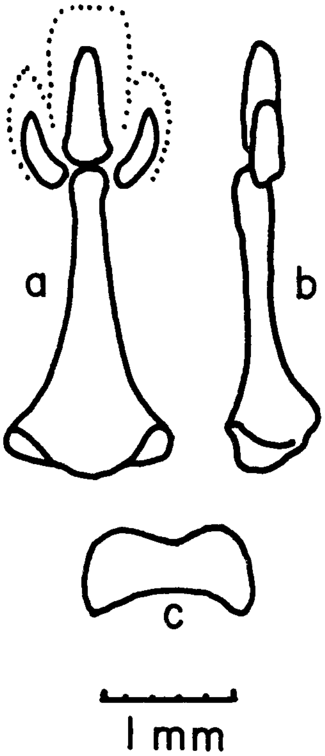

FIG. 4. Dorsal (a), right lateral (b), and proximal (c; dorsum upward) views of baculum of *Microtus oregoni*. Redrawn after Anderson (1960).

Other species of small mammals occurring in association with *M. oregoni* include: *Sorex vagrans*, *S. trowbridgii*, *S. bendirii*, *S. pacificus*, *Scapanus orarius*, *Neurotrichus gibbsii*, *Ochotona princeps*, *Sylvilagus bachmani*, *Lepus americanus*, *Aplodontia rufa*, *Thomomys mazama*, *Tamias townsendii*, *T. amoenus*, *Tamiasciurus douglasii*, *Spermophilus beecheyi*, *Glaucomys sabrinus*, *Peromyscus maniculatus*, *Neotoma cinerea*, *N. fuscipes*, *Microtus longicaudus*, *M. townsendii*, *M. canicaudus*, *M. richardsonii*, *M. californicus*, *Clethrionomys californicus*, *C. gapperi*, *Phenacomys albipes*, *Zapus trinotatus*, *Mustela erminea*, *M. frenata*, *Spilogale gracilis*, and *Mephitis mephitis* (Black and Hooven, 1974; Borrecco and Hooven, 1972; Gashwiler, 1959, 1970; Hawes, 1975; Maser and Hooven, 1969; Weil, 1975). Species not referenced but that likely occur in communities with creeping voles include: *Sorex monticolus*, *Scapanus townsendii*, *Thomomys talpoides*, and *Phenacomys intermedius*.

Although density of populations of *M. oregoni* seems related to seral stage, vegetative composition, and various forest management practices, separation of differences in density caused by these factors from those caused by use of different trapping regimes and models in various studies is difficult. On the basis of a 15-year study in Oregon conducted on a clear-cutting that supported a variety of forbs and shrubs but was relatively sparsely vegetated by grasses, population densities of *M. oregoni* estimated by the Lincoln Index ranged from 0 to 5/ha in spring and 0.7 to 15/ha in autumn (Gashwiler, 1972). Petticrew and Sadleir (1974:Fig. 2) reported that the minimum number of creeping voles known to be alive on a 1-

ha grid declined from about 39 in November 1968 to about 10 in June 1969, then increased to about 29 in December 1969 and declined to 0 in July 1970. By use of the same technique, Sullivan (1980:Fig. 2) estimated numbers to increase more or less continuously from 1 or 2 on a 1-ha grid in March to a maximum of about 34 in October 1978. Subsequently, he and a coworker reported the minimum number alive in an abandoned field surrounded by forest attained 72/ha (Sullivan and Krebs, 1981). The approximately 138/ha reported as the minimum number alive on a plot in British Columbia (Hawes, 1975:Fig. 4) seems to be the highest density recorded for the species. Hooven (1973) reported an annual catch of 9.5 individuals/ha in a 125-year-old Douglas fir (*Pseudotsuga menziesii*) stand, 27/ha in an unburned clear-cutting, and 54/ha in a clear-cutting on which slash was burned; in a similar study, 7.5/ha, 25/ha, and 47/ha were reported in the three habitat types, respectively (Hooven and Black, 1976). Hooven (1973) reported that the number of creeping voles caught in spring during a 3-year study always exceeded the number caught the previous autumn; however, Gashwiler (1972:Table 2) indicated greater densities in spring than the previous autumn during only 2 of 10 years. Gashwiler (1972) suggested that densities of populations occupying stages late in the forest sere were lower but more stable than those occupying recently disturbed sites.

Sullivan (1980), presumably by inspection of data presented by Gashwiler (1972), Hooven and Black (1976), and Petticrew and Sadleir (1974), suggested that populations of *M. oregoni* exhibited a 3- to 4-year cycle in abundance. Except for the study by Gashwiler (1972), the span of the studies was less than the length of the cycle suggested. Gashwiler's (1972:Fig. 1) records during a 15-year study indicated peak densities at 3, 8, and 11 years on clear-cuttings and at 4, 9, 10, and 12 years in virgin forest. Subsequently, Sullivan and Krebs (1981) provided evidence for cycles in the form of increase in weight of adult voles, sex ratios biased in favor of females, relative stability of habitats, and peaks in density of voles determined on different grids during overlapping studies. They concluded that populations of *M. oregoni* in old field habitats, and possibly those in early stages of the forest sere where *Microtus townsendii* was absent, exhibited a 3- to 4-year population cycle. Based on earlier studies conducted in the same area, Hawes (1975) concluded that populations of *M. oregoni* did not undergo typical cycles described for numerous other voles. Because of the rapidity with which densities of populations of creeping voles respond to manipulation of vegetation (Borrecco et al., 1979; Gashwiler, 1972; Hooven, 1973; Hooven and Black, 1976), and because of the absence of appropriate periodicity in peak numbers for a period longer than the proposed cycle, we suggest that multiannual cycles in *M. oregoni* populations remain to be established despite occurrence of significant increases in density from time to time.

The sex ratio of a wild-caught sample ($n = 713$) of creeping voles obtained in Oregon was 89 males/100 females (Gashwiler, 1972), whereas that of a sample ($n = 107$) obtained in British Columbia was 107 males/100 females (Cowan and Arsenault, 1954). Hooven (1973) suggested that samples collected in 1968 and 1969 in 125-year-old Douglas fir forest ($n = 6$ and $n = 15$) were biased toward males, and samples collected in two clear-cuttings ($n = 84$ and $n = 205$) were biased toward females; however, none of the sex ratios he presented was significantly different from 1:1 ($P < 0.05$). Redfield et al. (1978) reported extremely biased sex ratios in an unmanipulated population in British Columbia; during the nonbreeding season ($n = 150$) the sex ratio was 35 males/100 females, and during the breeding season ($n = 296$) it was 22 males/100 females. By manipulating sex ratios, Redfield et al. (1978) simulated removal of individuals from the population and increased the rate of recruitment of both sexes.

Minimum survival rates (proportion surviving 14 days) for adult creeping voles in British Columbia in summer ranged from 70 to 84% in old fields, 40 to 75% in grasslands, and 63 to 91% in brushlands; males generally had lower survival rates than females. Winter survival rates for age classes combined ranged from 55 to 80% in old fields, 70 to 77% in grasslands, and 65 to 87% in brushlands; again, males generally had lower survival rates than females (Sullivan and Krebs, 1981). Of 713 creeping voles captured 1,758 times, 49% were not recaptured after 1 month, 90% after 5 months, and 99% after 12 months (Gashwiler, 1972), supporting the contention of Cowan and Arsenault (1954) that nearly complete annual turnover in populations is common. However, in captivity, longevity of creeping voles may exceed 320 days frequently (Cowan and Arsenault, 1954), and Gashwiler (1972) reported that two wild females were alive 420 and 480 days after first capture.

Creeping voles primarily feed on green vegetation (presumably both forbs and grasses; Cowan and Arsenault, 1954; Hooven, 1973; Maser et al., 1978, 1981), but 36% by volume of stomach contents of 30 voles was fungi (Maser et al., 1978). Maser et al. (1978) suggested that replacement of *M. oregoni* in older stages of the sere by *Clethrionomys californicus* was related to food supply; old growth forests in the region contain few forbs and grasses for creeping voles, but an abundance of hypogeous mycorrhizal fungi that seemingly are requisite for red-backed voles. Other than its use of fungi, no quantitative evaluation of foods habits of *M. oregoni* is available.

Means of home-range areas for creeping voles in the Oregon Cascades calculated by the exclusive boundary-strip method ranged from 0.05 to 0.12 ha for males and 0.04 to 0.06 ha for females. Home-range size was least in summer for males and in autumn for females and greatest for both sexes in spring; estimates for winter were not available for females (Gashwiler, 1972). Hooven (1973), by use of the same method, estimated areas of 0.31 and 0.38 ha for males in the same region on burned and unburned clear-cuttings, respectively. For females, estimates of home-range size in the two habitat types were 0.18 and 0.23 ha.

Ectoparasites of *M. oregoni* include the coleopteran *Leptinus testaceus* (Maser and Hooven,1971); the louse *Hoplopleura acanthopus* (Emerson et al., 1984); the mites *Androlaelaps fahrenholzi*, *Eulaelaps stabularis*, *Haemogamasus occidentalis*, *Haemogamasus* sp., *Laelaps alaskensis*, *Radfordia hylandi*, *Dermacarus ondatrae*, *Glycyphagus hypudaei*, *Listrophorus mexicanus*, *Euryparasitus* sp., *Procotolaelaps* sp., and an unidentified member of the family Anoetidae (Whitaker and Maser, 1984); the chiggers *Euschoengastia oregonensis*, *Neotrombicula harperi*, and *N. cavicola* (Easton, 1975); and the following siphonapterans: *Atyphloceras multidentatus*, *Catallagia charlottensis*, *Doratopsylla jellisoni*, *Epitedia jordani*, *Hystrichopsylla gigas dippiei*, *Leptopsylla selenis*, *Megabothris abantis* (Hubbard, 1941), *Epitedia scapani*, *Peromyscopsylla selenis*, *Catallagia sculleni chamberlini*, *Delotelis hollandi*, *Hystrichopsylla o. occidentalis*, *Monopsyllus ciliatus protinus*, *Malaraeus telchinus* (Lewis and Maser, 1981), and *Malaraeus dobbsi* (Hubbard, 1940, 1941; Lewis, 1975).

Schlegel et al. (1968) did not record the trematode vector of "salmon-poisoning disease" (*Nanophyetus salmincola*) from creeping voles they examined.

In Oregon, remains of creeping voles occurred in 7% of 143 fecal passages of bobcats (*Felis rufus*) from the Coast Range and in 11.8% of 34 from the Cascade Mountains (Nussbaum and Maser, 1975). D. S. deCalesta (in litt.) recorded remains of *M. oregoni* in 6.0 to 10.5% of 247 fecal passages of bobcats and 5.0 to 12.5% of 309 fecal passages of coyotes (*Canis latrans*) in the Coast Range. He also found that the frequency of occurrence of *M. oregoni* in bobcat droppings was greatest in summer and fall, but least in spring; in coyote droppings, the frequency was greatest in winter and also least in spring. Sullivan and Sullivan (1980) concluded that introduction of seven ermines (*Mustela erminea*) to their 1-ha study plot did not result in a decline in density of the population of creeping voles, but, despite some ermines returning to their original home ranges, they speculated that the ermines possibly were responsible for the extirpation of the voles from the plot after numbers declined from other causes.

In Oregon, Giger (1965) found 22% of 2,886 small mammal skulls recovered from 724 regurgitated pellets of barn owls (*Tyto alba*) were those of *M. oregoni*, and Forsman and Maser (1970) reported 11% of 36 small mammal skulls recovered from 36 pellets of saw-whet owls (*Aegolius acadicus*) were *M. oregoni*. Maser and Brodie (1966) lumped all *Microtus* found in pellets of barn owls, long-eared owls (*Asio otus*), and great-horned owls (*Bubo virginianus*), but listed *M. oregoni* among the species represented. Likely other raptorial birds and carnivorous mammals prey on *M. oregoni*.

BEHAVIOR. Creeping voles are described as "burrowers" that construct subterranean tunnels in mellow forest soils; they sometimes push up ridges like miniatures of those made by some talpids (Bailey, 1936; Cowan and Arsenault, 1954; Maser et al., 1981). Ingles (1965) claimed the species constructed tunnels near the roots of grasses and seldom ventured outside of them. Conversely, Hooven (1973:262) reported that he was unable to find "burrows or surface tunnels that could be related to the vole" on his study area. Cowan and Arsenault (1954) stated that *M. oregoni* commonly used burrows of *Scapanus orarius* in British Columbia. Globular nests of grasses usually are constructed underground, but sometimes they are built on the surface under bark or inside decaying logs (Maser et al., 1981). Bailey (1936) contended that creeping voles were difficult to collect unless traps were set in their runways or tunnels. In our experience, creeping voles enter traps set where runways or tunnels are not conspicious; this combined with evidence derived from their remains in pellets of raptorial birds, suggests that activities of *M. oregoni* are not wholly subterranean as some authorities seemingly implied.

On the basis of a 4-year study of competition among four species of voles in British Columbia, Hawes (1975) concluded that vertical separation was necessary for coexistence of *M. townsendii* and *M. oregoni*; in flat areas, *M. townsendii* competed with *M. oregoni* by interference and *M. oregoni* avoided *M. townsendii* by constructing burrows too small for the latter species to enter. Where the water table was high, *M. oregoni* was unable to construct burrows, so was excluded from moist microhabitats by *M. townsendii*. Hawes (1975) believed that interactions between *M. oregoni* and *Clethrionomys gapperi* were minor and were mediated by the presence of *Peromyscus maniculatus*; also, he believed that *M. longicaudus* was excluded from some habitats by competition, but active interference by *M. oregoni* was not responsible.

Weil (1975) investigated agonistic interactions of *M. oregoni*, *M. townsendii*, and *M. canicaudus* by categorizing encounters with laboratory-reared animals in a neutral arena as dominant-subordinate, mutual avoidance, fraternal, or "no decision." Intraspecific encounters resulted in establishment of dominant-subordinate behavioral roles for about half of male-male and female-female pairings of *M. oregoni* but in more than 80% of male-female pairings; dominance over males was established by females in slightly more than half of the tests. In interspecific pairings irrespective of sex, *M. oregoni* and *M. canicaudus* exhibited about equal dominance, but in all encounters with *M. townsendii* except male-male pairings, *M. oregoni* was dominant. *M. oregoni* was the only species tested that exhibited a "jump attack" behavior.

GENETICS. *Microtus oregoni* may be unique among North American mammals in that both sexes are gonosomic mosaics; somatic and gonadal cells have different chromosomal complements (Ohno et al., 1963). The diploid number (2n) is 17 in females and 18 in males. There are 14 metacentrics and 2 submetacentrics; the sex chromosomes consist of a large submetacentric X and an acrocentric Y (Hsu and Benirschke, 1969). The somatic cells in the female are XO and the male XY; whereas, the gonadal cells are XX in the female and OY in the male (Hsu and Benirschke, 1969; Matthey, 1958; Ohno, 1967; Ohno et al., 1963, 1966). Although female determination is by sperm without a sex element, the female produces no O-bearing oöcytes that might unite with O-bearing or Y-bearing spermatozoa to produce lethal OY or OO zygotes (Ohno et al., 1963). "Instead, each oögonium receives two X-chromosomes by selective nondisjunction, so each ovulated oöcyte contains a haploid set with one X" (Ohno et al., 1963:238). Because the inert (positively heteropycnotic) X-chromosome found in somatic cells of most mammals has been eliminated, the sex-determining system in *Microtus oregoni* is considered to be the most advanced mammalian form (Ohno et al., 1963). Large differences (9%) in DNA content between the Y-bearing and O-bearing spermatozoa permitted Pinkel et al. (1982) to separate them by use of flow-sorting instrumentation. O'Farrell (1967) suggested that the low chromosome number in *Microtus oregoni* was responsible for its high susceptability to the effects of acute ionizing radiation.

Contrary to earlier interpretation (White, 1957), *Ellobius lutescens* and *M. oregoni* do not possess the same sex-determining mechanism; in *E. lutescens* males, 2n = 17 in somatic cells (Ohno et al., 1963).

REMARKS. Ognev (1950) considered *Microtus socialis* to belong to the subgenus *Chilotus* with *M. oregoni*, but, on the basis of karyotypes provided by Matthey (1953) of a small sample of presumed *M. socialis* from Iran, Anderson (1959) suggested that *M. socialis* should not be included in the subgenus *Chilotus*. Hooper and Hart (1962), on the basis of meibomian gland, cranial, and phallic characteristics, concluded that separation of *M. oregoni* by retention of the subgenus *Chilotus* was not warranted. Nevertheless, Chaline (1974) retained both *M. socialis* and *M. oregoni* in the subgenus *Chilotus*.

The generic name *Microtus* is from the Greek *mikros* meaning "small" and *otos* meaning "ear" (Jaeger, 1955); the specific name *oregoni* is from the state of Oregon in which the type specimen was collected.

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