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Microtus pennsylvanicus.

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Microtus pennsylvanicus (Ord, 1815)

Meadow Vole

Mus pennsylvanica Ord, 1815:292. Type locality meadows below Philadelphia, Pennsylvania.

M(icrotus) pennsylvanicus Rhoads, 1895:940. First use of current name combination.

Mynomes pratensis Rafinesque, 1817:45. Type locality meadows and seashore below Philadelphia, Pennsylvania.

Lemmus noveboracensis Rafinesque, 1820:3. Type locality New York or New Jersey.

Arvicola riparius Ord, 1825:305. Type locality not given.

Arvicola palustris Harlan, 1825:136. Type locality swamps along shores of Delaware River.

Arvicola hirsutis Emmons, 1840:60. Type locality Massachusetts.

Arvicola albo-rufescens Emmons, 1840:60. Type locality Williamstown, Massachusetts.

Arvicola fulva Audubon and Bachman, 1841:96. Type locality "One of the Western states; we believe Illinois."

Arvicola nasuta Audubon and Bachman, 1841:96. Type locality near Boston, Massachusetts.

Arvicola rufescens DeKay, 1842:85. Type locality Oneida Lake, New York.

Arvicola oneida DeKay, 1842:88. Type locality Oneida Lake, New York.

Arvicola drummondii Audubon and Bachman, 1854:166. Type locality "Valleys of the Rocky Mountains."

Arvicola dekayi Audubon and Bachman, 1854:298. Type locality New York or Illinois.

Arvicola modesta Baird, 1858:535. Type locality Cochetopa Pass, Saguache Co., Colorado.

Arvicola riparia var. *longipilis* Baird, 1858:524. Type locality West Northfield, Illinois or Racine, Wisconsin.

Arvicola rufidorsum Baird, 1858:526. Type locality Holmes Hole, Martha's Vineyard, Massachusetts.

Arvicola (Mynomes) aztecus Allen, 1893:73. Type locality Aztec, San Juan Co., New Mexico.

Arvicola insperatus Allen, 1894:347. Type locality Custer, Custer Co., South Dakota.

Arvicola (Mynomes) microcephalus Rhoads, 1894:286. Type locality Lac LaHache, British Columbia.

Arvicola terraenovae Bangs, 1894:129. Type locality Codroy, Newfoundland.

Microtus enixus Bangs, 1896*a*:1051. Type locality Hamilton Inlet, Labrador.

Microtus fontigenus Bangs, 1896*b*:48. Type locality Lake Edward, Quebec.

Microtus stonei Allen, 1899:5. Type locality Liard River, British Columbia.

Microtus aphorodemus Preble, 1902:52. Type locality 50 mi. S Cape Eskimo, near mouth Thlewiaza River, Keewatin.

Microtus provectus Bangs, 1908:20. Type locality Block Island, Newport Co., Rhode Island.

Microtus admiraltiae Heller, 1909:256. Type locality Windfall Harbor, Admiralty Island, Alaska.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Family Muridae, Subfamily Microtinae. The genus *Microtus* includes 8 subgenera, approximately 47 species, and 238 subspecies, distributed throughout the northern two-thirds of Eurasia, and in North America south to Guatemala. *M. pennsylvanicus* is included in the subgenus *Microtus* (Hall and Kelson, 1959; Ellerman and Morrison-Scott, 1951; Ellerman, 1940).

Recognized subspecies are (Hall and Kelson, 1959; Youngman, 1967; Bradley and Cockrum, 1968):

M. p. acadicus Bangs, 1897:239. Type locality Digby, Nova Scotia.

M. p. admiraltiae Heller, 1909:256, see above.

M. p. alcorni Baker, 1951:105. Type locality 6 mi. SW Kluane, Yukon.

M. p. aphorodemus Preble, 1902:521, see above.

M. p. arcticus Cowan, 1951:353. Type locality Kidluit Bay. Richards Island (69°31′N, 133°49′W) Mackenzie.

M. p. aztecus (Allen), 1893:73, see above.

M. p. chihuahuensis Bradley and Cockrum, 1968:1. Type locality 3 mi. SE Galeana, NW Chihuahua, Mexico.

M. p. copelandi Youngman, 1967:579. Type locality North Head, Grand Manan Island, New Brunswick.

M. p. drummondii Audubon and Bachman, 1854:166, see above. (*stonei* Allen is a synonym; *microcephalus* Rhoads, *rubidus* Dale, and *arcticus* Cowan may be synonyms.)

M. p. enixus Bangs, 1896*a*:1051, see above.

M. p. finitus Anderson, 1956:96. Type locality 5 mi. N, 2 mi. W Parks, Dundy Co., Nebraska.

M. p. fontigenus Bangs 1896*b*:48, see above.

M. p. funebris Dale, 1940:338. Type locality Coldstream, 3.5 mi. SE Vernon, British Columbia.

M. p. insperatus (Allen), 1894:347, see above.

M. p. kincaidi Dalquest, 1941:145. Type locality 10 mi. S Moses Lake, Grant Co., Washington.

M. p. labradorius Bailey, 1898:88. Type locality Fort Chimo, Quebec.

M. p. magdalensis Youngman, 1967:579. Type locality Grindstone Island, Magdalen Islands, Quebec.

M. p. microcephalus (Rhoads), 1894:286, see above.

M. p. modestus (Baird), 1858:535, see above. (*aztecus* Allen may be a synonym.)

M. p. nigrans Rhoads and Young, 1897:307. Type locality Currituck, Currituck Co., North Carolina.

M. p. pennsylvanicus (Ord), 1815:292, see above. (*pratensis* Rafinesque, *noveboracensis* Rafinesque, *riparius* Ord, *palustris* Harlan, *hirsutis* Emmons, *albo-rufescens* Emmons, *fulva* Audubon and Bachman, *nasuta* Audubon and Bachman, *rufescens* DeKay, *oneida* DeKay, *dekayi* Audubon and Bachman, *longipilis* Baird, and *rufidorsum* Baird are synonyms.)

M. p. provectus Bangs, 1908:20, see above.

M. p. pullatus Anderson, 1956:97. Type locality 12 mi. N and 2 mi. E Sage, Lincoln Co., Wyoming.

M. p. rubidus Dale, 1940:339. Type locality Sawmill Lake, near Telegraph Creek, British Columbia.

M. p. shattucki Howe, 1901:201. Type locality Tumble Down Dick Island, Penobscot Bay, Maine.

M. p. tananaensis Baker, 1951:107. Type locality Yerrick Creek, 21 mi. W, 4 mi. N Tok Junction, Alaska.

M. p. terraenovae (Bangs), 1894:129, see above.

M. p. uligocola Anderson, 1956:94. Type locality 6 mi. W, 0.5 mi. S Loveland, Larimer Co., Colorado.

Anderson and Hubbard (1971) placed *M. p. aztecus* within the synonymy of *M. p. modestus*, Martell (1975) placed *M. p. arcticus* within the synonymy of *M. p. drummondii*, Weaver (1940) placed *M. p. fontigenus* within the synonymy of *M. p. pennsylvanicus*, and Cowan and Guiguet (1956) placed *M. p. microcephalus* and *M. p. rubidus* within the synonymy of *M. p. drummondii*.

DIAGNOSIS. The following characters are diagnostic of *M. pennsylvanicus* (Hall and Kelson, 1959; Hall and Cockrum, 1953): first lower molar with 5 closed triangles, third lower molar with 3 transverse loops and no triangles, second upper molar with 4 closed triangles and a posterior loop, third upper molar with 3 closed triangles. Incisive foramen long and not constricted posteriorly. Nasals rounded posteriorly (Fig. 1). Plantar tubercles 6.

GENERAL CHARACTERS. External measurements in mm for adult *M. pennsylvanicus* (Fig. 2) vary as follows: total length, 140 to 195; length of tail, 33 to 64; length of hindfoot,18 to 24; length of ear, 12 to 16. The length of body is about 2 to 3 times the length of tail, and the tail is 1.9 to 2.7 times as long as the hindfoot. Mean (±SD) adult weight is 44.2 ± 6.29 g for males, and 44.0 ± 10.25 g for females. Cranial measurements (mm) for males (mean ± SD) are: greatest length of skull, 27.4 ± 0.63;

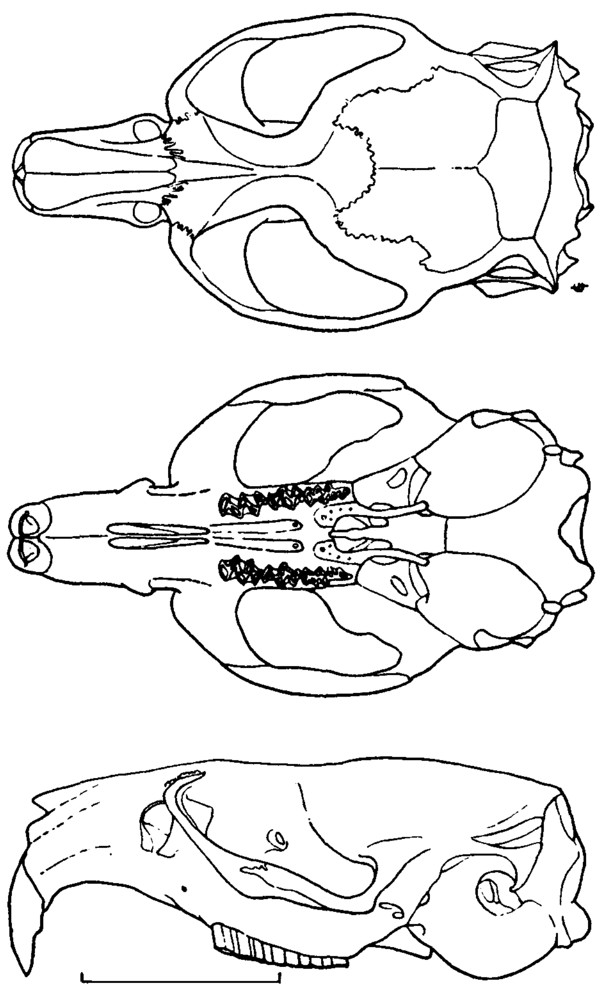

FIGURE 1. Dorsal, ventral, and lateral views of skull of male *Microtus pennsylvanicus pullatus* (from Hall and Kelson, 1959, by permission). Line at bottom represents 1 cm.

condylozygomatic length, 21.3 ± 0.52; length of nasal, 7.7 ± 0.42; length of incisive foramen, 5.2 ± 0.28; length of diastema, 8.3 ± 0.27; length of rostrum, 6.0 ± 0.23; cranial breadth, 11.0 ± 0.29; interorbital breadth, 3.7 ± 0.12; zygomatic breadth, 15.2 ± 0.47, and cranial height, 10.1 ± 0.27 (Hall and Kelson, 1959; Snyder, 1954). Adult males average slightly larger than females in cranial measurements (Snyder, 1954).

Upper parts vary in color from bright yellowish chestnut to dull bister with black-tipped hairs (Hall and Kelson, 1959). Northern subspecies were said to be more blackish or grayish (Hall and Kelson, 1959), although Hooper (1941) and Dale (1940) reported that southern forms were blacker. Burt and Grossenheider (1976) noted that western subspecies are notably lighter than eastern subspecies. The tail is bicolored. Pelage color varies with age, young animals being darker than older animals (Starrett, 1958). The sexes are colored alike (Starrett, 1958). Dale (1940) showed that body size increased along a cline from north to south and from high to low altitudes.

DISTRIBUTION. *Microtus pennsylvanicus* has the largest range of any American species in the genus *Microtus* (Fig. 3), occurring throughout Canada, the northern and eastern regions of the United States, and into Mexico (Hall and Kelson, 1959; Bradley and Cockrum, 1968; Youngman, 1967). It is most commonly found in grasslands, preferring moister areas, but may also be found in woodlands (Burt and Grossenheider, 1976).

FOSSIL RECORD. Martin (1968) summarized the Late Pleistocene records of *M. pennsylvanicus*, which has been reported from Florida, Louisiana, Texas, Kansas, Nebraska, Pennsylvania, Virginia, Indiana, Oklahoma, and Tennessee. Martin (1972) compared Pleistocene remains of *M. pennsylvanicus* with the extinct *M. paroperarius*, which he concluded is an ancestral form. Guthrie (1971) presented a model of the evolution of tooth cusp patterns in microtine rodents, and pointed out that no ancestor common to Old World and New World microtines is known.

FIGURE 2. Adult male *Microtus pennsylvanicus pennsylvanicus* from Plymouth, Massachusetts. (Photographed by the author and Peter V. August.)

FORM. The pelage of *M. pennsylvanicus* consists of two types of hair—short, flexible underhair (tricolored on the dorsum with dark gray bases, central bands of orange or yellow-brown, and short, dark tips, gradually becoming bicolored towards the venter, with gray bases and white tips) and longer, stiffer guard hairs (bicolored with short gray bases and long, dark brown tips), which occur predominantly on the dorsum (Starrett, 1958). The seasonal molt results from changes in the underhair with little change in the guard hair. Summer pelage is sparser and coarser than winter pelage (Starrett, 1958).

Anderson (1960) gave a detailed quantitative description and line drawings of the baculum, comparing it to those of other rodents. Snyder (1954) found considerable variability in linear cranial measurements within a population, and even greater variation between populations. By examining ontogenic variation, he concluded that the best craniometric characters for age determination are lengths of the paroccipital process and occipital crest. A detailed account of macro- and micro-anatomy of molars was presented in Phillips and Oxberry (1972). Oppenheimer (1965) studied within- and between-population variation in molar patterns, discussed the relationship between molar patterns and adaptive radiation, and suggested that there is a trend toward reduced molar complexity in microtine evolution. Guilday (1951) described sexual differences in innominate bone morphology.

The circulatory system was described on a biochemical level by Genaux and Morrison (1973), who constructed a complete peptide map of the hemoglobin of *M. pennsylvanicus*, and by Dieterich (1972) and Dieterich and Preston (1977), who reported on mean concentrations of various blood cells and plasma constituents. Carotid circulation was described by Guthrie (1963), and inner ear morphology by Hooper (1968).

Golley (1960*a*) reported both on macro- and micro-anatomical aspects of the digestive tract, including details of the mouth, tongue, esophagus, stomach, intestine, caecum, and liver. He found the caecum was unusually long and the colon and rectum were short. The large caecum is likely responsible for the high digestive efficiency (86 to 90%) of *M. pennsylvanicus*. Barry (1976) gave a histological description of the small intestine, and concluded that the villous and mucosal surface morphology was typical for an herbivore.

Zimny (1968) studied the renal glomerular capillaries, and concluded that the presence of an extracellular polysaccharide coat on the plasma membrane of the epithelial cells, and a central dense zone of basal lamina, are both adaptations to reduce urine output in cold weather.

Spermatogenesis was investigated by Beach (1931), and Arata (1964) described the structure of male accessory reproductive glands. There is one pair each of preputial, vesicular, and am-

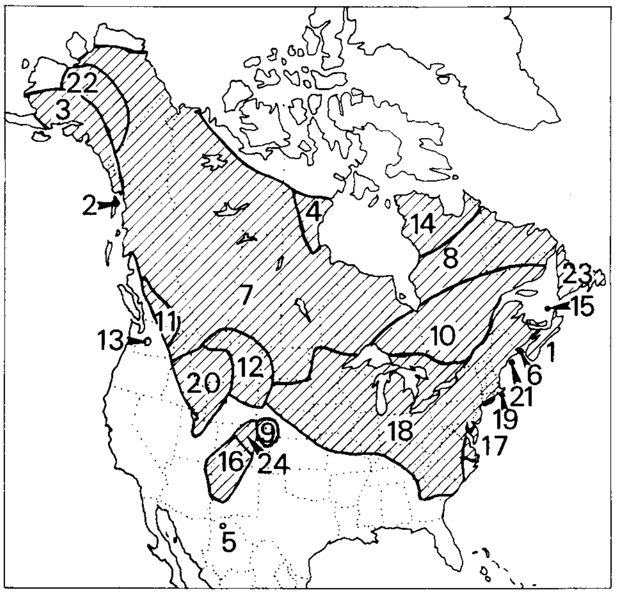

FIGURE 3. Distribution of *Microtus pennsylvanicus*, modified from Hall and Kelson, 1959 (Anderson and Hubbard, 1971; Bradley and Cockrum, 1968; Youngman, 1967). Subspecies are: 1, *M. p. acadicus*; 2, *M. p. admiraltiae*; 3, *M. p. alcorni*; 4, *M. p. aphorodemus*; 5, *M. p. chihuahuensis*; 6, *M. p. copelandi*; 7, *M. p. drummondii*; 8, *M. p. enixus*; 9, *M. p. finitus*; 10, *M. p. fontigenus*; 11, *M. p. funebris*; 12, *M. p. insperatus*; 13, *M. p. kincaidi*; 14, *M. p. labradorius*; 15, *M. p. magdalensis*; 16, *M. p. modestus*; 17, *M. p. nigrans*; 18, *M. p. pennsylvanicus*; 19, *M. p. provectus*; 20, *M. p. pullatus*; 21, *M. p. shattucki*; 22, *M. p. tananaensis*; 23, *M. p. terraenovae*; 24, *M. p. uligocola*.

pullary glands, and four pairs of prostate glands. The glans penis was described by Hooper and Hart (1962).

Christian and Davis (1966) noted that weight of adrenal glands of females increased sharply in response to estrogen secretion. Most variations in adrenal weight were due to changes in the cortical layer, primarily in the fasciculata and reticular zones. Cells of the hyperplastic inner cortical portion often contained small lipid vacuoles in the zona fasciculata, with fewer in the zona reticularis.

Dieterich and Preston (1977) reported on mean weights for many organs and organ systems of *M. pennsylvanicus*.

FUNCTION. The wound healing ability of *Microtus pennsylvanicus* was studied by Rose and Hueston (1978). Most skin punctures and scars were undetectable after one month.

Winter acclimatization and thermoregulatory strategies were studied by Narayansingh and Aleksiuk (1972), who described temperature-related changes in DNA and protein synthesis rates in the liver, small intestine, and brown fat masses, concluding that low ambient temperatures induce a reorganization of metabolic activity, such that energy available for heat production is maximized at the temporary expense of growth. Mean body weights are reduced in winter (Iverson and Turner, 1974). Brown fat weight decreases with higher body weight and higher ambient temperature (Didow and Hayward, 1969). The thermoneutral zone is 25 to 29°C (Wiegert, 1961). Pearson (1947) reported a 24-h mean oxygen consumption rate of 2.4 to 3.7 cc g^{-1} h^{-1}. Oxygen consumption is directly related to body weight, is highest at night, and decreases in response to huddling (Wiegert, 1961). Golley (1960*b*) reported a basal metabolic rate of 10 cal/day and an average tissue caloric value of 4.65 cal/g.

Holleman and Dieterich (1973) reported a mean total body water content of 63.0% body weight and a mean rate of water exchange of 8.1 ml/day. Getz (1963) found that evaporative water loss was 0.0125 g/cm^2 surface area per 6 h period at 28°C, and 0.0119 g/cm^2 at 33°C. Ernst (1968) calculated a water consumption rate of 0.21 ± 0.02 ml/g body weight/day.

Several studies found increased adrenocortical activity with increased population densities (Louch, 1958; Christian and Davis, 1966), although To and Tamarin (1977) presented evidence to the contrary. Seabloom (1965) found that peaks in adrenal activity corresponded with reduced motor activity and noted higher levels of corticosterone in females than in males. Seabloom et al. (1978) observed a spring peak in adrenal activity with a rapid decline into summer, except in subadult males, who showed an early summer peak. Levels of ACTH are higher in adults than in juveniles, and higher in non-pregnant females than in pregnant females (Seabloom et al. 1978). Olsen and Seabloom (1973) noted that confinement caused increased adrenal activity, especially in males. Ungar et al. (1978) determined that corticosterone is the major adrenal steroid produced. The weight of the thymus gland was lower at high population density, in winter months, and in breeding individuals, and arterial blood pressure was higher in artificial populations kept at high densities than at low densities (Blaine, 1973).

ONTOGENY AND REPRODUCTION. Copulation in *M. pennsylvanicus* consists of intra-vaginal thrusting, no lock, and multiple ejaculations (Gray and Dewsbury, 1975). First ejaculation is preceded by multiple intromissions, but subsequent ejaculations require only a single insertion. Ovulation is induced (Clulow and Mallory, 1974), and occurs 12 to 18 hours after coitus (Lee et al., 1970). A male-induced, pregnancy-block mechanism (the Bruce effect) was demonstrated by Mallory and Clulow (1977). Pre- and post-implantation mortality rates were estimated to be 0.3 and 0.1 ova per pregnancy, respectively (Tamarin, 1977*a*).

Gestation is 21 days (Dieterich and Preston, 1977). Manly (1953) described parturition. The six young in the litter he observed were all born within 40 minutes; birth of a litter observed by Hamilton (1941) took 7 hours. Manly (1953) observed the mother construct a nest and place the neonates within it in the 2 hour period following parturition. Using radio-telemetry, Madison (1978*a*) noted that female movement sharply decreased at parturition. Mean litter sizes range from 4.0 to 6.2, with extremes of one to 11 young per litter (Hamilton, 1941; Kott and Robinson, 1963; Tamarin, 1977*a*). Litter size is not significantly correlated with latitude or elevation (Innes, 1978). Keller and Krebs (1970) noted that fall, winter, and spring litters averaged 14% smaller than summer litters. They also noted that litter size was positively correlated with body size, was not significantly different in primiparous and multiparous females, and was constant in summer breeding periods at different population densities.

Neonates of *M. pennsylvanicus* are pink and hairless, with closed eyes and ear pinnae, and weigh from 1.6 to 3.0 g (Hamilton, 1941). Fur begins to appear at day 4, and the entire body with the exception of the belly is covered with juvenile hair by day 7. The eyes and ears open by day 8, and vocalization ability appears at day 4 (Hamilton, 1941; Manly, 1953). Pepin and Baron (1978) described the development of motor activity during the first 21 days. According to Hamilton (1941), weaning occurs between 12 and 14 days after birth. An average of 2.6 young per litter (63% of the litter) is successfully weaned (Morrison et al. 1976).

Getz (1960) reported a mortality rate of 88% for the first 30 days after birth, and Krebs et al. (1969) found that early juvenile mortality was not related to changes in population density. Growth rates for the first 25 to 30 days after birth range from 0.2 to 0.5 g per day (Barbehenn, 1955) to 1 g per day (Hamilton, 1941). Brown (1973) found that young born in spring and early summer attained adult weight in 12 weeks, and underwent a fall weight loss. Young born in late summer continued growing into the fall, and maintained their weight through the winter. Myers and Krebs (1971*a*) reported a more rapid growth rate in juvenile males than in juvenile females.

Reproductive rate is sensitive to adrenal activity (Pasley, 1974), and depends on season and population density, with winter breeding occurring at high population density (Tamarin, 1977*a*), particularly in individuals of greater body weight (Keller and Krebs, 1970). Tamarin (1977*a*) estimated an average pregnancy rate of 60%. Post-partum estrus was observed in 55% of the females in a laboratory colony (Morrison et al., 1976).

Estimates of mean longevity range from 2 to 3 months (Beer and MacLeod, 1961) to 10 to 16 months (Hamilton, 1941). Survival rates for laboratory bred voles for a period of 144 weeks were given in Morrison et al. (1977). For field populations, Tamarin (1977*b*) determined that females had greater survival rates than males, but juvenile survival rates did not vary with sex.

ECOLOGY. *Microtus pennsylvanicus* is locally sympatric with a variety of small mammals over its wide geographic range. This vole is often restricted to moister habitats when sympatric with *M. ochrogaster* or *M. montanus* (Findley, 1954), and excludes *Clethrionomys gapperi*, *Peromyscus leucopus*, and *P. maniculatus* from grasslands (Morris and Grant, 1972; Bowker and Pearson, 1975; Grant, 1971). *M. pennsylvanicus* also coexists with *Sigmodon hispidus*, *Zapus hudsonius*, *Synaptomys cooperi*, and *Oryzomys palustris* (Terman and Johnson, 1971; Shure, 1971; Getz, 1961*a*; Harris, 1953). *M. pennsylvanicus* appears to avoid locations frequented by *Blarina brevicauda* in the field, and avoids its scent in the laboratory (Fulk, 1972). Annual population densities of *M. pennsylvanicus* seem to be inversely related to the number of short-tailed shrews present (Eadie, 1952).

Microtus pennsylvanicus is prey for many hawks, owls, and carnivores, and is also taken by some snakes (Madison, 1978*b*). *Blarina brevicauda* may be a predator (Eadie, 1952). There is extensive documentation of ecto- and endo-parasites (for example, Kinsella, 1967; Rausch and Tiner, 1949; Whitaker and Wilson, 1974; Timm, 1973). These parasites include several species of the following groups: trematodes, cestodes, nematodes, acanthocephalans, anoplura, siphonaptera, diptera, and acarina. The ecology of botfly (*Cuterebra*) infection was studied by Getz (1970*a*). Protozoan, bacterial, and viral infections have been reported (Kirner et al., 1958; Whitney et al., 1970).

Microtus pennsylvanicus populations are characterized by cyclic fluctuations in density with a period of 2 to 5 years. These cycles were summarized by Krebs and Myers (1974). Many factors have been mentioned as being important in the population regulation of microtine rodents. Batzli and Pitelka (1971) suggested that food quality is important, with population cycles being caused by a lag in nutrient-recovery time. Pearson (1966) stressed the importance of predation in microtine cycles, noting that predators are responsible for determining the timing and the amplitude of the cycle in *M. californicus*. Krebs and Myers (1974) describe how climatic events can be of importance in the timing of various demographic changes. Christian (1970) emphasized the importance of physiological stress, noting that an increase in population density raises the level of endocrine stress in the population, which ultimately results in a decline in density. Chitty (1967) and Krebs et al. (1973) suggested that behavioral and genetic factors are important in causing cyclic fluctuations. The behavior-genetic model of Chitty (1967) maintains that at different population densities selection differentially favors voles which differ in their respective genetically-determined intraspecific behavior. Changes in behavior and gene frequencies of electrophoretic loci have been observed (Krebs et al., 1973). The importance of dispersal as a regulation factor was discussed by Krebs et al. (1973) and Tamarin (1977*c*). Normal population cycles do not occur when dispersal is prevented, and under normal conditions, dispersers have been shown to be behaviorally, genetically, and demographically different from residents.

The dispersal tendency of *M. pennsylvanicus* is well documented. Myers and Krebs (1971*b*) and Reich and Tamarin (1980) noted behavioral differences between dispersing and resident subpopulations of *M. pennsylvanicus*, and differences in frequencies of alleles have been noted by Keith and Tamarin (In press) and Myers and Krebs (1971*b*). Tamarin (1977*b*) noted seasonally related size differences in dispersers and residents, and observed that males contributed a disproportionately larger portion of the dispersal population in the winter, whereas females were more common among dispersers in summer. A positive relationship between dispersal rate and population density was noted by Tamarin (1977*b*). Hilborn (1975) emphasized the similarity in dispersal tendency between siblings, especially during population increases. Grant (1978) studied dispersal in relation to carrying capacity and energetics.

A review of home range dynamics was provided by Van Vleck (1969), who reported home ranges of 405 to 3,480 m^2 (0.10 to 0.86 acres) for males, and 160 to 3,115 m^2 (0.04 to 0.77 acres) for females. Home range size depends on season (summer ranges are larger than winter ranges), habitat (ranges in marshes are larger than ranges in meadows), and population density (ranges are smaller at higher population densities) (Tamarin, 1977*c*; Getz, 1961*b*). Getz (1961*b*) observed that roughly 20% of the population (mostly males) shifted their home range each month. Getz (1961*b*) estimated the size of a defended area to be less than 7 m in diameter, and found that the degree of territoriality was independent of population density or environmental conditions.

Robinson and Falls (1965) studied the homing ability of *M. pennsylvanicus*, and noted no successful homing at a displacement distance of greater than 305 m. They concluded that homing is accomplished through prior knowledge of the terrain and through random wandering. The ability of *M. pennsylvanicus* to use the sun for sun-compass orientation was demonstrated by Fluharty et al. (1976).

Microtus pennsylvanicus appears to eat most available species of grasses, sedges, and herbaceous plants. Riewe (1973) found that herbaceous vegetation is eaten primarily in summer and autumn. He recorded 64 vascular and 9 non-vascular plant species in the diet, and noted that among the plants eaten, many are typical of the forest. Zimmerman (1965) found that the grasses *Poa*, *Panicum*, and *Muhlenbergia* predominated in the diet. The occurrence of fungi, primarily *Endogone*, in the diet of *M. pennsylvanicus* has been noted (Bakerspigel, 1956). Meadow voles also eat insects (Zimmerman, 1965), and sometimes scavenge on animal remains (Riewe, 1973). At high population densities, *M. pennsylvanicus* may seriously damage woody vegetation, especially in fruit orchards, by girdling (Byers, 1979).

By studying mineral levels in stomach contents, Bergeron (1976) determined that nitrogen, calcium, phosphorus, and magnesium levels are a function of the concentrations in food plants while potassium levels are consistent throughout the year. Grant (1978) proposed several methods by which *M. pennsylvanicus* can minimize mineral deficiencies.

Habitat selection may be influenced by relative ground cover of grasses and herbs (Getz, 1970*b*), soil moisture (Wrigley, 1974), soil sodium levels (Aumann and Emlen, 1965), soil pH and potassium levels (Krebs et al., 1971), surface temperature and humidity (Getz, 1971), and inter-specific competition (Grant, 1971). Woodland populations have a lower reproductive success and lower adult survival rates than do grassland populations (Grant, 1975).

Maintenance of *M. pennsylvanicus* as a laboratory animal was described by Lee and Horvath (1969). Meadow voles were found to be useful as bioassay organisms to test for the nutritive quality of, and presence of toxins in, food plants (Schillinger and Elliott, 1966; Kendall and Sherwood, 1975). Chemical regulation of vole populations in commercial fruit orchards was discussed in Byers (1979).

BEHAVIOR. *Microtus pennsylvanicus* acts aggressively in intraspecific encounters (Getz, 1962). Intraspecific male aggression varies directly with population density (Krebs, 1970), and reproductive activity (Turner and Iverson, 1973). In interspecific encounters, *M. pennsylvanicus* was subordinate to other *Microtus* species (D. Colvin, 1973).

Microtus pennsylvanicus can be active at any time of day although short-term activity cycles with a mean of 4.8 h (Ambrose, 1973) have been reported. Ambrose (1973) determined that at any given moment at least 50% of the population was active. Kavanau and Havenhill (1976) found a dual light-preference curve, with activity peaks at darkness and at 15% starlight. Voles may be more active in the daytime (Ambrose, 1973) or at night (Seabloom, 1965). Graham (1968) suggested that the time of major activity depends on the amount of vegetative cover present. Under dense cover activity will be mostly diurnal, whereas under sparse cover, activity will be mostly crepuscular. Getz (1961*c*) noted that *M. pennsylvanicus* switched from diurnal to nocturnal activity when ambient temperatures were above 20°C, but that they were not active when temperatures dropped below 0°C. Voles were more active during a new moon than during a full moon, regardless of nighttime cloud cover (Doucet and Bider, 1969). Myers and Krebs (1971*b*) found a greater level of activity in dispersing voles compared to resident voles, and Ambrose (1973) found a positive correlation between activity and population density.

Krebs (1970) observed that vocalizations often accompany aggressive threats. The average threat vocalization has a duration of 0.068 seconds, has a fundamental frequency of 1.5 kHz, and a maximum frequency of 1.8 kHz (Houseknecht, 1968). There are few vocalizations in interspecific encounters (Houseknecht, 1968). M. Colvin (1973) found that ultrasonic vocalizations were produced in response to a variety of stressful conditions, and described four acoustically distinct calls.

Microtus pennsylvanicus may select foods based on low alkaloid content (Kendall and Sherwood, 1975), low fiber content (Keys and Van Soest, 1970), and high nutritive quality (Schillinger and Elliott, 1966). Voles can detect the presence of various solutes added to their drinking water (Laughlin et al., 1975).

Weilert and Shump (1977) described nest-building and the physical parameters of the nest.

GENETICS. The transferrin (Tf) locus consists of 6 alleles, and is inherited as a codominant, autosomal trait (Gaines and Krebs, 1971). Maurer (1969) studied temporal and geographic variation at this locus in 24 separate populations from North Dakota to Massachusetts. He found no evidence of temporal variation, but did detect macrogeographic trends in the frequencies of certain alleles and significant microgeographic differences in three populations in New York. Gaines and Krebs (1971) determined that the leucine amino peptidase (LAP) locus was dimorphic and was controlled by two codominant autosomal alleles. Changes in the allele frequencies at the transferrin and leucine amino peptidase loci are correlated with differences in population density, sex, survival rates, growth rates, breeding activity index, body weights, and resident or dispersing individuals (Gaines and Krebs, 1971; Myers and Krebs, 1971*b*; Tamarin and Krebs, 1969; Kohn and Tamarin, 1978; Birdsall, 1974). Kohn and Tamarin (1978) studied a total of 15 loci, and except for Tf and LAP, all were monomorphic. A case of dimorphism at the hemoglobin (Hb) locus was noted for *M. pennsylvanicus* from Montana (Stratton and Duffy, 1976), and the 6-phosphogluconate dehydrogenase (6PGD) locus was found to be dimorphic in *M. pennsylvanicus* from Nebraska (Nadler et al., 1978).

Little (1958) summarized coat color mutations and assigned them to probable loci known from other rodents. The following mutations were described: yellow (A^y), brown (b), complete albino (C^a), himalayan rabbit (C^H), extreme dilute (c^e), blue dilute (d), yellow (e), pink-eye (p), extreme white piebald (s^w), and black-eyed white (W). Barrett (1976) found a population in Ohio with the extreme dilute phenotype in 5 of 19 individuals. Breeding experiments suggested that the trait was inherited as a recessive.

Microtus pennsylvanicus has a diploid chromosome number of 46 with a fundamental number of 50. Its autosomes consist of two pairs of large subtelocentrics, one pair of large metacentrics, and 19 pairs of small to large telocentrics. The X is a large subtelocentric and the Y is a small telocentric (Hsu and Benirschke, 1967).

REMARKS. The genus name *Microtus* is derived from the Greek micro (small) and otus (ear). The species name is derived from Pennsylvania, the state from which the species was first described.

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