

Reithrodontomys megalotis. By Wm. David Webster and J. Knox Jones, Jr.

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Reithrodontomys megalotis (Baird, 1858)

Western Harvest Mouse

- Reithrodon megalotis* Baird, 1858:451. Type locality between Janos, Chihuahua, and San Luis Springs, Grant Co., New Mexico.
- Reithrodontomys megalotis* Allen, 1893:79; first use of current name combination.
- Reithrodontomys longicauda* Baird, 1858:451. Type locality Petaluma, Sonoma Co., California.
- Reithrodontomys aztecus* Allen, 1893:79. Type locality La Plata, San Juan Co., New Mexico.
- Reithrodontomys pallidus* Rhoads, 1893:835. Type locality Santa Ysabel, San Jacinto Mts., San Diego Co., California.
- Reithrodontomys dychei* Allen, 1895:120. Type locality Lawrence, Douglas Co., Kansas.
- Reithrodontomys arizonensis* Allen, 1895:134. Type locality Rock Creek, 8,000 ft, Chiricahua Mts., Cochise Co., Arizona.
- Reithrodontomys saturatus* Allen and Chapman, 1897:201. Type locality Las Vigas, 8,000 ft, Veracruz.
- Reithrodontomys klamathensis* Merriam, 1899:93. Type locality Big Spring, Shasta Valley, Siskiyou Co., California.
- Rhithrodontomys peninsulæ* Elliot, 1903:164. Type locality San Quintín, Baja California del Norte.
- Rhithrodontomys catalinae* Elliot, 1904:246. Type locality Santa Catalina Island, Santa Barbara Islands, California.
- Reithrodontomys amoles* Howell, 1914:40. Type locality Pinal de Amoles, about 7,500 ft, Querétaro.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Cricetinae, Tribe Hesperomyini. Sixteen subspecies (but see Remarks section) of *R. megalotis* currently are recognized (Hall and Kelson, 1959; Jones and Mursaloğlu, 1961), as follows:

- R. m. alticolus* Merriam, 1901:556. Type locality Cerro San Felipe, 10,000 ft, Oaxaca.
- R. m. amoles* Howell, 1914:40, see above.
- R. m. arizonensis* Allen, 1895:134, see above.
- R. m. aztecus* Allen, 1893:79, see above (*caryi* Howell is a synonym).
- R. m. catalinae* (Elliot, 1904:246), see above.
- R. m. distichlis* von Bloeker, 1937:155. Type locality salt marsh at mouth of Salinas River, Monterey Co., California.
- R. m. dychei* Allen, 1895:120, see above (*nebrascensis* Allen and *pectoralis* Hanson are synonyms).
- R. m. hooperi* Goodwin, 1954:1. Type locality Rancho del Cielo, 5 mi NW Gómez Farías, 3,500 ft, Tamaulipas.
- R. m. limicola* von Bloeker, 1932:133. Type locality Playa del Rey, Los Angeles Co., California.
- R. m. longicaudus* (Baird, 1858:451), see above (*klamathensis* Merriam and *pallidus* Rhoads are synonyms).
- R. m. megalotis* (Baird, 1858:451), see above (*deserti* Allen, *nigrescens* Howell, and *sestiniensis* Allen are synonyms).
- R. m. peninsulæ* (Elliot, 1903:164), see above.
- R. m. ravus* Goldman, 1939:355. Type locality north end of Stansbury Island, 4,250 ft, Great Salt Lake, Tooele Co., Utah.
- R. m. santacruzæ* Pearson, 1951:366. Type locality Prisoners Harbor, Santa Cruz Island, Santa Barbara Co., California.
- R. m. saturatus* Allen and Chapman, 1897:201, see above (*cinereus* Merriam is a synonym).
- R. m. zacatecae* Merriam, 1901:557. Type locality Sierra de Valparaíso, Zacatecas (*obscurus* Merriam is a synonym).

DIAGNOSIS. *Reithrodontomys megalotis* (Fig. 1) is a small, long-tailed rodent with medial grooves on the anterior surface of the upper incisors. The ears are prominent; the tail is slender, scaly, and scantily haired. Western harvest mice have six tubercles on the soles of the hindfeet, and three pairs of mammae, one pectoral and two inguinal. The braincase (Fig. 2) is rounded and

smooth; the zygomata are slender, but possess broad zygomatic plates. The long incisive foramina are separated by a thin septum and terminate anterior to the maxillary toothrow. The pterygoids are nearly parallel and the pterygoid fossae are broad. The posterior border of the palate is truncate. The tympanic bullae are moderately inflated and angled obliquely to the longitudinal axis of the skull. The coronoid process is reduced. The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16.

Two subgenera of New World harvest mice, *Reithrodontomys* and *Aporodon*, currently are recognized. The former includes *R. megalotis* and is distinguished cranially from the latter (Hooper, 1952; Howell, 1914) as follows: zygomatic plate broader than mesopterygoid fossa; mesopterygoid fossa narrower, equal in width to the crown length of M2; pterygoid fossa more than twice as broad as mesopterygoid fossa, and pterygoid hamulae inflated slightly and not reflexed laterally. *Reithrodontomys* also has a simpler molar pattern than *Aporodon*, with reduced mesolophids (mesolophids) and mesostyles (mesostylids), and an incomplete third molar. Additionally, the zygomasseteric musculature of *Reithrodontomys* is distinct from that of *Aporodon* (Rinker and Hooper, 1950).

It sometimes is difficult to distinguish *R. megalotis* from other members of the subgenus. "There are no absolute characters by which this species can be distinguished from certain congeners; usually close comparison must be made and identification based on the summation of characters" (Hall and Kelson, 1959). Breadth of braincase separates *R. megalotis* (10.7 mm or less) from *R. chrysopsis* and *R. sumichrasti* (greater than 10.7). The third molar in *R. megalotis* has a faint or absent first primary fold that always is shorter than the second primary fold, whereas *R. fulvescens* and *R. hirsutus* have a well-developed first primary fold. *R. burti*, *R. humulis*, and *R. montanus* are smaller than *R. megalotis*. The latter differs from *R. raviventris* in that the total pelage is shorter and the ears are buffy to reddish-brown rather than blackish; also, the tail of *megalotis* is more distinctly bicolored. See Hall (1981), Hall and Kelson (1959), and Hooper (1952) for diagnostic keys to the species of harvest mice.

GENERAL CHARACTERS. The dorsal pelage is one of two types, grayish to blackish guard hairs that are less numerous than shorter cover hairs. The latter are gray basally, with a buffy terminal band or a buffy subterminal band and a black terminal tip. In addition, *R. m. dychei* east of the Missouri River (Hoffmeister and Warnock, 1955) and *R. m. hooperi* from southwestern



FIGURE 1. *Reithrodontomys megalotis dychei* from Lawrence, Douglas Co., Kansas.



FIGURE 2. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw of *Reithrodontomys megalotis megalotis* (TTU 32227, female) from 6 mi N, 6 mi E Ft. Davis, Jeff Davis Co., Texas. The greatest length of skull is 21.9 mm.

Tamaulipas (Goodwin, 1954) frequently have a buffy pectoral spot, as do many individuals of *R. m. longicaudus* from the San Francisco Bay area (Fisler, 1965). Albinism is a rare recessive condition similar to that found in *Mus* (Egoscue, 1958).

Selected average and extreme external and cranial measurements (mm) from a series ($n = 85$) of *R. megalotis* from Indiana (Whitaker and Mumford, 1972), followed by one ($n = 15$) from western Texas and another ($n = 11$) from southern Oaxaca, both after Hooper (1952), are, respectively: total length, 126.8 (114 to 146), 133 (120 to 152), 144 (135 to 154); length of tail, 58.3 (50 to 69), 68 (61 to 78), 73 (64 to 83); length of hindfoot, 16.3 (15 to 18), 17 (16 to 18), 17 (15 to 18); length of ear from notch, —, 14 (12 to 15), 14 (13 to 15); greatest length of skull, 20.4 (19.0 to 21.4), 20.5 (19.6 to 21.2), 21.3 (20.0 to 22.5); zygomatic breadth, —, 10.4 (10.0 to 11.0), 10.5 (10.1 to 10.8); breadth of braincase, 10.0 (9.6 to 10.7), 9.9 (9.5 to 10.3), 9.7 (9.0 to 10.1); interorbital breadth, 3.2 (2.7 to 3.8), 3.0 (2.9 to 3.2), 3.0 (2.8 to 3.2); length of palate, 3.6 (3.2 to 4.0), 3.4 (3.2 to 3.7), 3.3 (2.9 to 3.5); length of maxillary toothrow, 3.1 (2.8 to 3.5), 3.3 (3.2 to 3.5), 3.3 (3.0 to 3.4).

Fisler (1965) and Jones and Mursaloglu (1961) listed measurements for large series from California and the Central Great Plains, respectively. The latter authors found secondary sexual variation in mensural characters to be less than individual variation in populations on the Great Plains.

DISTRIBUTION. The distribution of the western harvest mouse is mapped in Fig. 3. It is known from southwestern Canada (British Columbia, Alberta, and Saskatchewan) southward to southern México (Oaxaca and Veracruz), and from California eastward to recently-invaded Indiana (Ford, 1977; Whitaker and Mumford, 1972).

The species is known altitudinally from 250 feet (about 77 m) below sea level at Death Valley, California, to approximately

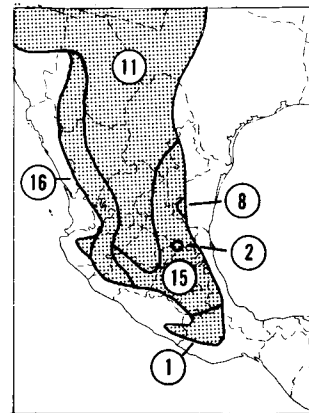
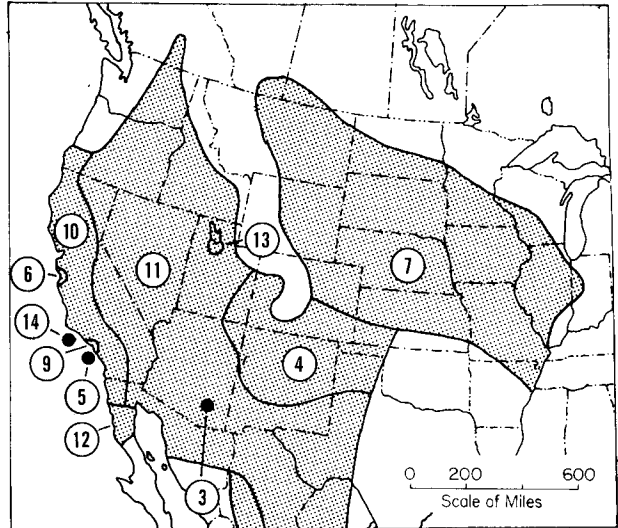


FIGURE 3. Distribution of *Reithrodontomys megalotis* in Canada and the United States (above) and México (below). Subspecies are: 1, *R. m. alticola*; 2, *R. m. amoles*; 3, *R. m. arizonensis*; 4, *R. m. aztecus*; 5, *R. m. catalinae*; 6, *R. m. distichlis*; 7, *R. m. dychei*; 8, *R. m. hooperi*; 9, *R. m. limicola*; 10, *R. m. longicaudus*; 11, *R. m. megalotis*; 12, *R. m. peninsulæ*; 13, *R. m. ravus*; 14, *R. m. santacruzæ*; 15, *R. m. saturatus*; and 16, *R. m. zacatecæ*. Note that the ranges of *saturatus* and *zacatecæ* are thought to overlap in Jalisco.

13,000 feet (4,000 m) on volcanos Popocatepetl and Orizaba in México (Hooper, 1952).

FOSSIL RECORD. *Reithrodontomys cf. megalotis* is known from Sangamon fossil beds in the Cragin Quarry Fauna, Kansas (Hibbard and Taylor, 1960). Illinoian remains from the Mt. Scott Fauna, Kansas, are referable to *Reithrodontomys*, and have styles and stylids similar to those of *megalotis* (Hibbard, 1963). Jakway (1958) assigned late Pleistocene remains from San Josecito Cave, Nuevo León, to *R. megalotis*.

FORM. The glans penis and os penis, figured by Hooper (1959) and Burt (1960), respectively, are morphologically similar to those of *Peromyscus*. The elongate phallus is rod-shaped and four to five times greater in length (6.0 mm) than in diameter (1.3 mm). The shaft is armored with small proximally-directed spines, but the terminal segment is aspinous. The os penis is a simple bone of uniform thickness that gradually arches upward from a dorsoventrally flattened and laterally expanded base; it lacks a cartilagenous tip. Geographic variation in total length of baculum (6.2 to 9.2 mm) and basal width (0.5 to 1.1 mm) is moderate, with specimens from México averaging slightly larger than those from the United States (Burt, 1960).

Males have a well-developed vesicular, paired ampullary and Cowper's glands, and four pairs of ventral prostate glands; however, they lack preputial glands (Arata, 1964). Average vagina length of seven estrus females was 17.3 mm (Fisler, 1965). The

hyoid apparatus, albeit slightly smaller, is similar to that of the subgenus *Peromyscus* (Sprague, 1941). There are small sebaceous, sudoriferous, and mucous glands associated with the buccal cavity (Quay, 1965). Small intestine and recto-colon lengths are 3.1 and 1.4 times that of the body length, respectively (Fisler, 1965).

FUNCTION. According to Fisler (1965), western harvest mice maintain a normal body temperature (35 to 38°C) when exposed to variable laboratory temperatures (17 to 29°C); however, individuals kept at 4.8°C for 14.5 h became torpid with a rectal temperature of 26.5°C. Hibernation has been reported in Nevada (O'Farrell, 1974), and in captive animals torpor has been recorded (Coulombe, 1970) in response to osmotic stress or water deprivation.

Pearson (1960) found the minimum oxygen consumption for *R. megalotis* to be 2.5 cc g⁻¹ h⁻¹ at an ambient temperature of 33°C, with a metabolic increase of 0.27 cc g⁻¹ h⁻¹ for each 1°C decrease in ambient temperature. Also, oxygen consumption decreased if mice huddled or utilized a nest, but increased approximately 35% in experimental animals from which the fur had been removed.

Adult and fetal body compositions (percent dry weight) are, respectively: water, 68 and 88; ash, 14 and 11; lipid, 21 and one (Flehart et al., 1973). Adult lipid content, however, is higher in winter than summer. Western harvest mice preferably consumed fresh water during controlled experiments, but some salt water can be tolerated (Fisler, 1963). In fact, *R. m. limicola* consumed approximately twice as much 25% sea water than tap water in such experiments, and maintained constant body weight on 1.0 M NaCl solution (MacMillen, 1964). Western harvest mice have an exceptionally high evaporative water loss of 1.35 mg H₂O/cc O₂ consumed (Coulombe, 1970), and may reduce water loss in salt marshes by concentrating urine chlorides (MacMillen, 1964).

R. megalotis can perceive soundwaves of 35,000 and 23,000 vibrations per second on hot-dry and cold-rainy days, respectively (Davis, 1927). Young mice squeak frequently, but adult vocalizations are rare unless courting, fighting, or injured.

ONTOGENY AND REPRODUCTION. Most reproductive activity occurs from early spring to late autumn, with reduced midsummer activity, but these mice do breed year-round in the warmer parts of their geographic range. Females become sexually mature in just over four months of age and are polyestrous. Each of two females kept in optimal captive conditions gave birth to 14 litters in a single year (Bancroft, 1967); one produced a total of 58 young (litter size ranged from two to six) and the other 57 (litter size two to five).

Males are polygamous, and dominant males copulate with females in estrus (Fisler, 1965). The male venter contacts the female lower back when copulating; there is no locking or thrusting. Ejaculation occurs after the first intromission and multiple ejaculations are possible (Dewsbury, 1975). Postpartum estrus is known.

One to nine fetuses (Long, 1962) have been reported; 75 pregnant females from Nebraska had an average of 4.3 (Jones, 1964), whereas 41 from California averaged 3.8 (Fisler, 1965). Young are born after a gestation period of 23 to 24 days. Neonates are pink, hairless (except vibrissae), and have closed eyes and ears. They weigh 1.0 to 1.5 g and are 7.0 to 8.0 mm in length at birth (Jackson, 1961). Lightly haired young begin to crawl after five days and have erupting mandibular incisors (Smith, 1936; Svihla, 1931). The eyes and ears open between day 11 and 12, and weaning is complete in 24 days. The sex ratio evidently is about even at birth, but males were found by Fisler (1971) to predominate in all age classes thereafter except among old animals, when there was a predominance of females.

Western harvest mice have three characteristic pelages during their lifetime. The juvenile pelage is short, relatively sparse, and grayish brown. Postjuvenile molt "occurs at an early age, perhaps frequently before the young leave the nest" (Jones and Mursaloğlu, 1961). The subadult pelage is thicker, longer, and brighter than that of juveniles but duller than the pelage of adults.

Adults molt twice annually—in spring and autumn (Jones and Mursaloğlu, 1961). Spring molt proceeds posteriorly on the dorsum and venter, the latter being completed first. Autumnal molt is irregular. Molt is delayed in pregnant or lactating females. In summer the dorsal pelage is short (5 to 6 mm), sparse, and brownish to dark brownish on the dorsum, sides, and flanks; the venter is grayish. The pelage of winter is long (8 to 9 mm), denser, buffy dorsally and laterally, and the venter is whitish; also, the tail is more distinctly bicolored in the winter.

Senility in western harvest mice begins to occur at about 45

weeks of age and is accompanied by reduced litter size in females (Bancroft, 1967). Jones and Mursaloğlu (1961) suggested that old animals may have difficulty in completing seasonal molt. Fisler (1971) found essentially a complete turnover of individuals annually in California populations, few mice reaching the age of 12 months.

ECOLOGY. Western harvest mice typically inhabit grassy and weedy habitats such as overgrown pastures, meadows, fence-rows, fallow fields, and borders of agricultural and riparian areas, and not infrequently represent one of the most common mammals in such habitats. Individuals also are known from deserts, salt marshes, and pine-oak forests. *R. megalotis* is partially sympatric with at least eight other species of harvest mice, and although "there are records of occurrence of *megalotis* with each of these species" (Hooper, 1952), it is separated ecologically from *raviventris* (Fisler, 1965) and *montanus* (Hill and Hibbard, 1943). Multiple captures with *R. fulvescens* and *Baiomys taylori* have been reported in live traps in Durango (Peterson, 1975).

Spherical nests usually are located on the ground under heavy grass, bushes, weeds, or fallen logs, and are approximately 125 mm in diameter. Some nests are built (up to 1 m) above the ground in small shrubs. The nest is composed of plant fibers with an inner layer of finer plant "down." There are one or more openings near the base. Individuals have been reported as nesting in burrows in Illinois (Birkenholz, 1967).

Meserve (1977) reported circular or elliptical home ranges in California that averaged about 3,525 m². Density estimates vary from 4.8 per acre (about 11.9 per ha) in Washington (Gray, 1943) to 4.0 per ha in New Mexico (Whitford, 1976); the New Mexico population, however, increased to 60 per ha when ground vegetation became dense after September rains. Fisler (1966) recorded 330 feet (about 102 m) as the farthest distance between captured points of mice on a study area in California, although Brant (1962) earlier estimated 225 feet (about 70 m) as the average maximum distance between captures for *R. megalotis*. "Homing" ability was demonstrated by mice displaced by Fisler (1966) up to 1,000 feet (about 308 m) from their home areas.

This species is primarily granivorous, but individuals also consume herbaceous material and lepidopteran larvae (Meserve, 1976; Whitaker and Mumford, 1972). Natural predators include owls, hawks, snakes, canids, mustelids, felids, and scorpions (Hall, 1946). Cannibalism infrequently occurs among cagemates; in fact, *R. megalotis* is among the most tolerant of small mammals in that individuals in captivity frequently huddle together and even do so with mice of other species. When placed in an artificial enclosure with *Onychomys leucogaster*, western harvest mice were killed within three hours (Ruffer, 1968). No antagonistic behavior was reported when caged under conventional conditions with *Mus musculus* (Catlett and Shellhammer, 1962); however, water deprivation resulted in cooperative interspecific attacks and cannibalism on female *R. megalotis* and then on female *M. musculus*. *R. megalotis* frequently uses the runways of *Microtus* and *Sigmodon* (Hall, 1946), but does not assist in runway maintenance (Pearson, 1959). There appears to be no tendency for western harvest mice to avoid *Microtus* in Californian runways (Pearson, 1960a).

Numerous parasites are reported from *Reithrodontomys megalotis*. Endoparasites include the protozoan *Trypanosoma* sp. (Davis, 1952), acanthocephalan *Moniliformis clarkii* (McKeever, 1963), cestode *Hymenolepis diminuta*, and nematodes *Syphacia obveleta* and *Rictularia coloradensis* (Rankin, 1945). Ectoparasites found on western harvest mice include fleas (Siphonaptera) *Epitedia wenmani* and *Orchopeas leucopus*, and chiggers (Acarina) *Leeuwenhoekia americana*, *Trombicula alfreddugesi*, *T. lipovskyi*, *T. peromysci*, *T. diversa*, and *T. hungerfordi* (Loomis, 1956), and *Trombicula autumnalis* and *T. loomisi* (Kardos, 1954). Mites (Acarina) known to occur on *Reithrodontomys megalotis* include *Dermacarus* sp., *Androlaelaps fahrenheitii*, *Radfordia subuliger*, *Myocoptes* sp., *Hirstionyssus incomptus*, *H. occidentalis*, *H. eutimiae*, *H. isabellinus*, *H. tricanthus*, *H. utahensis*, *Macrocheles* sp., *Eubrachylaeps debilis*, and *Myobia musculi* (Whitaker and Mumford, 1972). Verts (1960) also reported *Heplopleura hesperomydis* (Anopleura).

BEHAVIOR. Western harvest mice are nocturnal, and more active on moonless and rainy nights in California (Pearson, 1960a). In addition, increased activity was apparent when live traps were set adjacent to rodent runways.

Holes in nests are repaired immediately and, because several nests are constructed and utilized on different occasions, only old nests are fouled with excrement. "Breeding females are partic-



FIGURE 4. Karyotype of *Reithrodontomys megalotis megalotis* (TTU 4678, male) from Mt. Locke, Ft. Davis State Park, Jeff Davis Co., Texas. Note the three supernumerary chromosomes. Photograph courtesy of Robert J. Baker.

ularly careful in nest building and repair" (Fisler, 1965). He found *R. megalotis* to be more "tense" than *R. raviventris*. For example, when placed in water, *R. megalotis* swam erratically, did not use its tail to facilitate swimming, and struggled to keep its head above water. Also, as compared to the aforementioned species, *R. megalotis* attempted frequent escapes from captivity and, when successful, darted directly to the nearest cover.

GENETICS. The basic diploid number of chromosomes in *Reithrodontomys megalotis* is 42, although up to four supernumerary chromosomes may be present (Blanks and Shellhammer, 1968; Matthey, 1961). The basic complement of 40 autosomes includes 18 metacentrics, 16 submetacentrics, and six subtolocentrics. The X-chromosome is submetacentric and the Y-chromosome is subtolocentric (Shellhammer, 1967). The karyotype of *R. m. megalotis* from Texas shown in Fig. 4 includes three supernumeraries.

REMARKS. *Reithrodontomys* combines three Greek words to mean "grove-toothed mouse." The specific name *megalotis* is derived from the Greek words *mega* and *otis*, "large eared."

We recognize only 16 subspecies of *R. megalotis* although Hall (1981) listed 17. Following Jackson (1961), he included *R. m. pectoralis*, which we regard as a synonym of *R. m. dychei* (see Hoffmeister and Warnock, 1955).

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