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Reithrodontomys humulis.

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Reithrodontomys humulis (Audubon and Bachman, 1841)

Eastern Harvest Mouse

Mus humulis Audubon and Bachman, 1841:97. Type locality "in the vicinity of Charleston," Charleston County, South Carolina.
Mus carolinensis Audubon and Bachman, 1842:306. Type locality "South Carolina" (may refer to this species).
Mus LeContii Audubon and Bachman, 1842:307. Type locality "Liberty County, Georgia."
Reithrodontomys merriami Allen, 1895:119. Type locality "Austin Bayou, near Alvin, Bazoria County Texas."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Muridae, Subfamily Sigmodontinae (Musser and Carleton, 1993), Genus *Reithrodontomys*, Subgenus *Reithrodontomys*. There are 20 recognized species in this genus (Musser and Carleton, 1993). Three subspecies of *R. humulis* are recognized (Hall, 1981):

R. h. humulis Audubon and Bachman, 1841:97, see above. Includes *carolinensis*, *lecontei*, *dickinsoni*, and *impiger*.
R. h. merriami Allen, 1895:119, see above.
R. h. virginianus Howell, 1940:346. Type from "Amelia, Amelia County, Virginia."

DIAGNOSIS. Of the five species of *Reithrodontomys* in the United States, the range of *R. humulis* significantly overlaps only that of *R. fulvescens*. Small areas of overlap occur with *R. megalotis* in northeastern Arkansas and with *R. montanus* in northwestern Arkansas and southeastern Oklahoma. *R. humulis* is notably smaller than *R. fulvescens*, as shown by ranges of external measurements (in mm) for *R. humulis* and *R. fulvescens*, respectively: total length, 107–128, 134–200; length of tail, 45–60, 72–116; length of hind foot 15–17, 16–22; length of ear, 8–9, 11–17 (Hall, 1981). The pelage of *R. humulis* is less reddish, with a dark mid-dorsal stripe typically absent in *R. fulvescens*. In *R. fulvescens* the first primary fold of M3 is at least as long as the second primary fold, with each usually extending >50% across the crown. In *R. humulis* the primary fold is shorter and extends <50% across the crown (Hooper, 1952). *R. megalotis* differs from *R. humulis* by having a tail length equal to or longer than the length of head and body. The tail is more sharply bicolored in *R. montanus* than in *R. humulis*. In addition, the labial fold and coalescence of folds on M1 and M2 differentiate *R. humulis* from *R. megalotis* and *R. montanus*.

GENERAL CHARACTERS. *Reithrodontomys humulis* is a small mouse with upper parts a rich brown, sometimes faintly washed with gray, and a dark mid-dorsal stripe (usually present; Fig. 1). Sides are paler than the dorsum, with an obvious lateral line usually present. Underparts are ash-colored and often have a cinnamon or pinkish suffusion. The slender, sparsely-furred tail is bicolored, fuscous to dark brown above and grayish white below. The soles of the hind feet have six tubercles (Hall, 1981).

Reithrodontomys humulis has ears that are fuscous or fuscous-black in color and feet that are grayish-white (Howell, 1914). Immature specimens are more fuscous above than adults, with a slight admixture of brown. *R. h. merriami* has less brown (thus more black and gray) on the upper parts than other subspecies, and its ears are smaller and blacker. In *R. h. virginianus*, the pelage is paler and more grayish, a distinct band of blackish brown occurs mediolaterally on the back, the ears are fuscous, and the feet white (Howell, 1940).

The skull of *R. humulis* (Fig. 2) ". . . is relatively small with a highly arched, narrow braincase; nasals and rostrum are short, broad; zygomata parallel or slightly narrower anteriorly" (Hall, 1981:637). The nasals narrow markedly posteriorly, the rostrum is narrowest above the preorbital fossa and constitutes no more than 82% of the interorbital breadth, and the interpterygoid fossae are moderately broad—from 1.3 to 1.5 times the greatest breadth of the incisive foramen (Hooper, 1943).

External and skull measurements (in mm; means, followed by range for the species in parentheses) of adults of *R. h. merriami* (n = 4), *R. h. humulis* (n = 5), and *R. h. virginianus* (n = 4), respectively, are as follows: total length, 126, 125, 122 (116–135); length of tail, 61, 62, 53 (47–68); length of hind foot, 15.9, 16.5, 16.0 (14.5–17.0); condylobasal length, 17.7, 17.2, 17.0 (16.8–17.9); depth of cranium, 7.5, 7.4, 7.6 (7.0–7.7); zygomatic breadth, 9.7, 9.4, 9.7 (9.3–10.1); interorbital constriction, 3.0, 2.8, 2.9 (2.7–3.1); nasal length, 7.1, 7.2, 7.0 (6.5–7.5); length of incisive foramen, 3.8, 3.8, 3.7 (3.6–3.9); length of hard palate, 3.4, 3.2, 3.2 (3.0–3.5); alveolar length of molar row, 3.0, 2.7, 2.9 (2.6–3.2—Hooper, 1943).

Except during pregnancy, field-caught adults in Tennessee average ca. 8.2 g with males ranging from 6.6 to 8.1 g and females from 7.2 to 11.7 g (Dunaway, 1968). Thus mean weights for sexes are most similar from February through April. No sexual difference in weights for laboratory-raised animals up to 50 days of age were found (Kaye, 1961*a*).

DISTRIBUTION. *Reithrodontomys humulis* occurs primarily in the southeastern United States (Fig. 3); however, a lack of trapping records is apparent in several key areas of this distribution. The gaps may represent true absence of the species, but in many instances they probably represent the lack of adequate collecting. *R. humulis* has extended its range in historic time; Hooper (1943) attributed this expansion to man's clearing of forest lands, cultivation of gramineous crops, and subsequent abandonment of fields that furnish adequate cover and seed production.

FOSSIL RECORD. The fossil record for the genus *Reithrodontomys* in North America extends back to the early Blancan Pliocene (with four extinct species named), but *R. humulis* is first recognized in the late Irvingtonian (middle Pleistocene). Six fossil faunas from Florida that contain *R. humulis* range in age from the late Irvingtonian to the Rancholabrean (Kurtén and Anderson, 1980).

A single jaw from Kanopolis, a late Irvingtonian interglacial fauna in central Kansas, was referred to *R. humulis* (Hibbard et al., 1979). This site is >240 km from the nearest modern record (Fig. 3). Specimens from the Costeau Pit in Los Angeles County California (late Illinoian or Sangamonian age) were tentatively referred to this species by Miller (1971), but due to the distance from extant records, they remain problematic.

FORM AND FUNCTION. Three varieties of glands are found in the oral lips and angle in *R. humulis*—sebaceous types

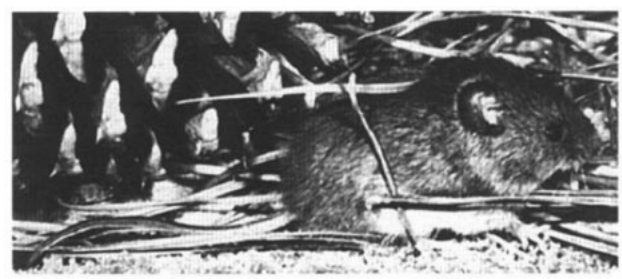

FIG. 1. Adult *Reithrodontomys humulis*. Photograph by R. W. Van Devender.

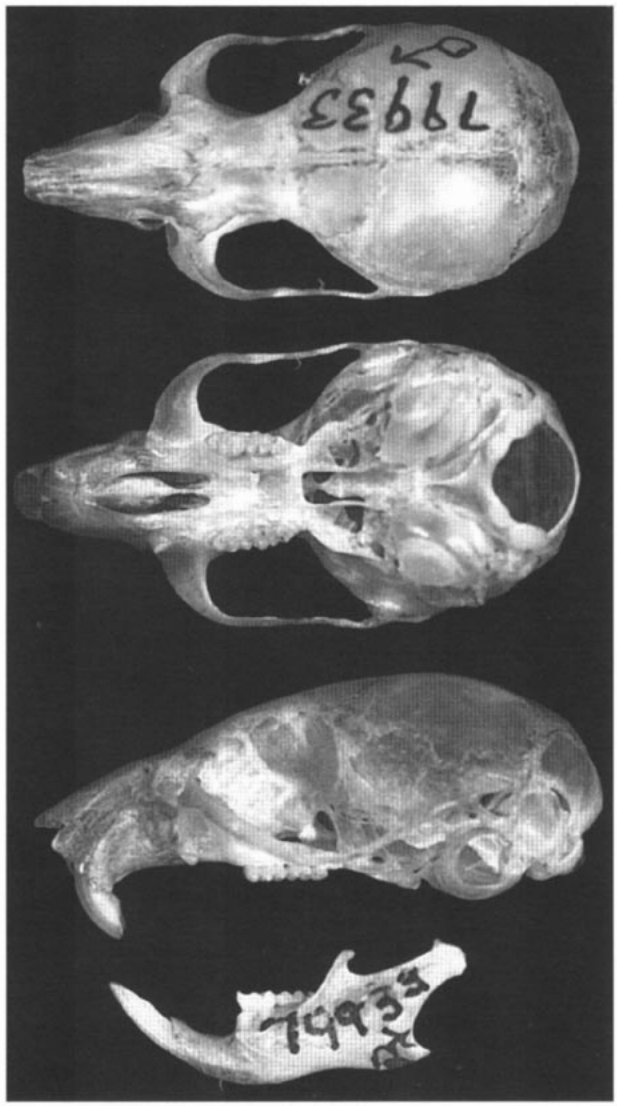

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of *Reithrodontomys humulis humulis* from near Morton, Scott Co., Mississippi (male, University of Kansas Museum of Natural History 79933). Greatest length of skull is 19.0 mm. Photographs by Mark Bills.

in intermediate amounts, and sudoriferous and mucous types in trace amounts (Quay, 1965). Compared with gland densities of 13 related species, *R. humulis* lies in the middle of the range. One pair of mammae is pectoral and two pairs are inguinal.

When Carleton (1973) examined gross stomach morphology of 10 species of *Reithrodontomys*, he found considerable specific variation in stomach shapes. *R. humulis* and *R. montanus* most closely agree in stomach shape and in the lining border fold that separates regions of cornified and glandular epithelium.

The baculum of *R. humulis* is a slender rod with a relatively small base, it is moderately curved dorsoventrally, and bacular length is 13.5 times the greatest basal width (Blair, 1942). This ratio is greater than that noted by Blair (1942) for 12 species of the genus *Peromyscus*, the northern grasshopper mouse (*Onychomys leucogaster*), and the pygmy mouse (*Baiomys taylori*). The length of the baculum in *R. humulis* is 8.5% of the animal's body length (Blair, 1942). The glans penis of *R. humulis* most closely resembles that of *R. megalotis*; however, it differs in being shorter and larger in diameter (Hooper, 1959). The dental formula of the eastern harvest mouse is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Lowery, 1974).

Small size in mammals is associated with increased metabolic rate (Eckert et al., 1988). Resting metabolism in *R. humulis* at 23°C is 4.35 cc O_2 g^{-1} hr^{-1}, but at 7°C it is 9.62 cc O_2 g^{-1} hr^{-1}

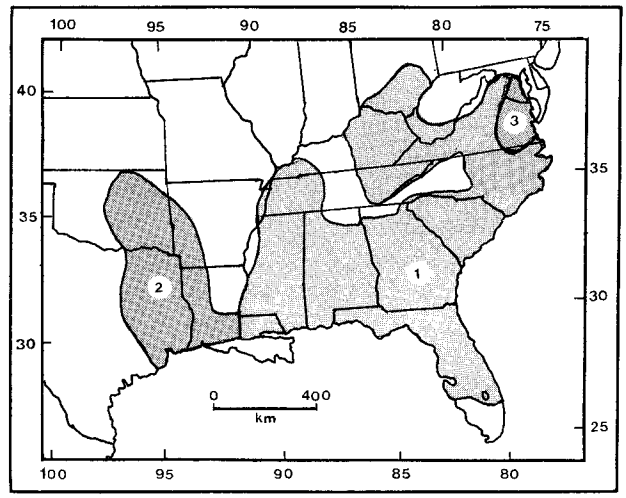

FIG. 3. Distribution of *Reithrodontomys humulis* in the United States (modified from Hall, 1981, with addition of peripheral trap records from >40 publications and personal correspondence): 1, *R. h. humulis*; 2, *R. h. merriami*; 3, *R. h. virginianus*.

(Dunaway, 1968). Comparatively, in the larger white-footed mouse (*Peromyscus leucopus*), metabolic rate at 24°C is 3.04 cc O_2 g^{-1} hr^{-1}, but at 8°C it is only 5.68 cc O_2 g^{-1} hr^{-1} (Dunaway, 1968). Thus for a 16°C difference in temperature, the metabolic rate of *R. humulis* changes by a factor of 2.21, while that of *P. leucopus* changes by a factor of 1.87. Dunaway (1968) speculated that the large increase in metabolic rate of *R. humulis* at lower temperatures may account in part for seasonal home range shifts, significant population decreases during the winter, and habitat selection reported for this species.

The mean metabolic rates of kidney and liver tissue from *R. humulis* were found to be ca. 17.0 and 6.7 ml O_2 mg of dry tissue^{-1} hr^{-1}, respectively (Redmond and Layne, 1958). When these data are compared to data for three other mammals (white mouse, white rat, and domestic rabbit) on a logarithmic plot, the kidney data approximate values expected, relative to body size, but the liver data are below expected levels. *R. humulis* hemoglobin at pH 6.8 is 50% saturated at a partial pressure of 32.2 mm Hg for oxygen (Foreman, 1954). This value is lower than that for several larger, related rodents (*Peromyscus leucopus*, 33.2 mm Hg; *Ochrotomys nuttalli*, 36.7 mm Hg). The oxygen-hemoglobin dissociation curve for *R. humulis* also falls higher on the Y-axis (saturation) than would predicted from body size. Other blood parameters for *R. humulis* include erythrocyte count, 9.56×10^6 cells/mm^3; hemoglobin, 15.51 g/100 ml; hematocrit, 43.57%; and mean erythrocyte diameter, 5.95 μm (Foreman, 1956). In contrast, an erythrocyte count of 12.34×10^6 cells/mm^3 and a hemoglobin concentration of 18.12 g/100 ml blood, as well as a mean corpuscular volume of 39 μm^3 have also been reported (Dunaway, 1968). Differences in hydration levels may explain the discrepancies (Stalling and Haines, 1982).

ONTOGENY AND REPRODUCTION. *Reithrodontomys humulis* has reproductive peaks in spring and autumn, with reduced effort in the summer (Cawthorn and Rose, 1989—in Virginia; Dunaway, 1968—in Tennessee; Packard, 1968—in Texas). Eighty percent of females collected in Virginia during the autumn (August-November) were pregnant (Chandler, 1984). In the southern part of the range during favorable years, breeding probably occurs throughout the year (Lowery, 1974). Dunaway (1968) reported only two January pregnancies in Tennessee. In the Great Dismal Swamp of southeastern Virginia, 93% of male *R. humulis* had scrotal testes in the summer and 24% in the winter (Stankavich, 1984). Scrotal males were found every month of the year in Virginia, but during the winter only 10% of males were scrotal (Chandler, 1984). In Tennessee no scrotal males were reported during January, February, or March (Dunaway, 1968).

Gestation period for the eastern harvest mouse is estimated to be 21 days (Kaye, 1961*a*) and <24 days (Layne, 1959). Ages at first pregnancy in two captive females housed with mature males were 11 and 20 weeks; intervals between litters for one female

varied from 24 to 49 days (Layne, 1959). Neither Layne (1959) nor Kaye (1961*a*) noted a postpartum estrus, but the minimal litter interval suggests the possibility.

In the laboratory, litter sizes for *R. humulis* range from 1 to 8, with means for litters conceived in the field of 2.2–3.7 and for litters conceived in the laboratory of 2.9–3.2 (Dunaway, 1968). Mean reproductive efficiency (total litter weight as a fraction of weight of mother) for laboratory-born litters was 43.7% (n = 4) with a range of 30.8–50.5% (Kaye, 1961*a*). Reproductive efficiencies of most mammals are ≤33% (Frank, 1957).

Mean neonatal birth weight is 1.2 g in *R. humulis* in North Carolina (Kaye, 1961*a*) and in Florida (Layne, 1959). Weight gain occurs in four phases, with highest rates in phase I (birth-10 days), followed by phase III (23–40 days), phase II (11–22 days), and phase IV (40 days to maturity—Kaye, 1961*a*). Weight gain slows significantly by 7 weeks and ends by 9 weeks (Kaye, 1961*a*; Layne 1959). Mean external measurements (in mm) for three freshly-killed newborns were as follows: total length, 37.3; length of tail, 10.7; length of hind foot, 5.3 (Layne, 1959).

The pinna is folded at birth and measures ca. 0.3 mm (ear crown to tip—Kaye, 1961*a*). At 1 week of age it is erect and measures ca. 5.0 mm (from notch—Layne, 1959). No significant growth in pinna or hind foot occurs after 4 weeks, and growth in total length is completed by 9 weeks. Tail lengthening is completed by 5 weeks; at 4 days of age the prehensile nature of the tail is apparent (Layne, 1959). Eyelids open at 7–13 days and the external auditory meatus at 7–11 days. Weaning starts ca. day 9, with completion by the 23d day.

Pelage development in *R. humulis* has been described by Hooper (1952), Layne (1959), and Kaye (1961*a*). At birth the young appear unpigmented with nearly microscopic white natal hair covering much of the body. One day after birth the dorsum darkens, with density and pigmentation of mid-dorsal and nape hair increasing until day 5 when the nape shows a brownish tinge. White hair also grows on the venter and legs. By the fifth or sixth day epidermal scales appear on the head and back. By the eighth day the darker dorsum is distinctly separated from the grayish white underparts. By 10 days the pelage is developed enough to suggest the gray juvenile pelage of most *Peromyscus*. At this age the underfur is more dense, as its growth is more rapid than that of the guard hairs. By the end of the second week, the juvenile pelage is almost fully developed and gives the animal a fuzzy, less sleek appearance. During the fourth week, buff-colored hairs become prominent on the venter and ferruginous hairs on the sides. The post-juvenile molt is first observed in young 4 weeks old, but not completed by all young until the ninth week. Subadult pelage is browner above and more buffy along the lower sides; venter pelage becomes whiter and thicker. Full adult pelage is not obtained for one more molt (perhaps two in some individuals) and occurs before 30 weeks of age (Layne, 1959). Pelage replacement in general proceeds as in the post-juvenile molt, with the brownish and buffy areas becoming more intense. The rump is usually the first area to develop the adult color, followed by the area from rump to shoulders. Adult *R. humulis* undergo two partial or complete molts a year (Hooper, 1943). Sexual dimorphism in coat color has not been reported.

In the field young *R. humulis* leave the nest at 30 days of age (Chandler, 1984). However, laboratory-raised young were first observed outside the nest with parents at 2 weeks of age, and were regularly foraging outside the nest at 3–4 weeks of age (Layne, 1959). One 4-week-old mouse had only solid food in its digestive tract (Layne, 1959). Apparent discrepancies in age of independence may be explained by trap-avoidance in juveniles, which has also been noted in pregnant adults (Chandler, 1984). Young do not leave the nest until relatively large, and with only two exceptions, field-captured animals weighed ≥5 g (Dunaway, 1968).

ECOLOGY. The habitat is commonly described as old field in studies where *R. humulis* is a sizable component of the small mammal population. Golley (1962:114) described eastern harvest mouse habitat in Georgia as ". . .abandoned fields in the late herbaceous and early broomsedge stages of old-field succession, roadside ditches, thickets, honeysuckle thickets, and wet meadows." In Ohio *R. humulis* is found in abandoned fields of corn (*Zea mays*) or timothy (*Phleum pratense*), with the following genera of herbs occurring most commonly: *Solidago*, *Aster*, *Physalis*, *Veronia*, *Ambrosia*, *Plantago*, *Solanum*, and *Elymus* (Gottschang, 1965). In Texas, Wilkins (1991) trapped *R. humulis* in grasslands in which principal grasses were little bluestem (*Schizachyrium scoparium*) and indiangrass (*Sorghastrum nutans*); secondary grasses were big bluestem (*Andropogon gerardii*), tall dropseed (*Sporobolus asper*), switchgrass (*Panicum virgatum*), and eastern gamagrass (*Tripsacum dactyloides*). Scattered woody vegetation included bois-d'arc trees (*Maclura pomifera*), sugarberry trees (*Celtis laevigata*), coral berry (*Symphoricarpos orbiculatus*), and poison ivy (*Toxicodendron radicans*). In Virginia *R. humulis* was found in old fields containing several different habitats (Chandler, 1984). In wetter areas spikerush (*Juncus*) and bulrush (*Scirpus*) dominated, whereas in drier areas broomsedge (*Andropogon virginicus*) did. Small saplings of sassafras (*Sassafras albidum*) and black cherry (*Prunus serotina*) were scattered throughout the fields. Major forbs that were present were goldenrods (*Solidago*), asters (*Aster*), and dog fennel (*Eupatorium capillifolium*). Small regions were dominated by Japanese and coral honeysuckles (*Lonicera japonica* and *L. sempervirens*). In a 2-year study in Tennessee, >350 *R. humulis* were captured in old-field habitats dominated by red-top (*Triodia*) and goldenrod (*Solidago*); the grass genera of primary importance were *Andropogon*, *Triodia*, and *Digitaria* (Dunaway, 1968). In north-central Oklahoma specimens were captured in the Tallgrass Prairie Rolling Hills physiognomic region characterized by primarily the same species of grass as Wilkins (1991) identified in Texas (Thies et al., 1993).

Eastern harvest mice are commonly found in areas with dense vegetation, at and near the ground. Composition of plant species apparently is of little importance in defining the microhabitat of *R. humulis* (Cawthorn and Rose, 1989), as has also been found for other species of *Reithrodontomys* (Ford, 1977; Spencer and Cameron, 1982; Wilkins, 1986).

The natural diet of *R. humulis* is not well known, but in the laboratory it thrives on shelled corn, sunflower seeds, crimped and flaked oats, Purina lab chow, grass seeds, and various fresh fruits and vegetables (Gottschang, 1981; Kaye, 1961*a*; Layne, 1959). In natural populations, weed and grass seeds, small green vegetation, and orthopterous insects constitute the majority of the diet (Dunaway, 1968; Lowery, 1974; Sealander and Heidt, 1990).

Sex ratios (male:female) reported for laboratory-born *R. humulis* range from 1:1 (Layne, 1959) to 1:1.51 (Kaye, 1961*a*). Sex ratios in field studies where >20 individuals were trapped varied in both directions: 1:0.86 (Chandler, 1984); 1:1.23 (Dunaway, 1968); 1:0.71 (Shadowen, 1956); and 1:1.21 (Stankavich, 1984). Dunaway (1968) in Tennessee and Chandler (1984) and Rose (1986) in Virginia, noted that females become difficult to trap during the primary time of pregnancy (June-August). At other times of the year, trappability is similar in both sexes. There are reports of reduced success in trapping females after parturition but of increased trappability of both sexes during winter months, leading to artificially high estimates of population (Cawthorn and Rose, 1989). Juveniles are captured consistently from July to December (Chandler, 1984).

Population densities reported for *R. humulis* vary considerably, with a high of 44.4/ha (Chandler, 1984) to a low of 8.75/ha (Dunaway, 1968). This difference may in part be due to habitat, but is probably largely due to differences in trapping techniques (Cawthorn and Rose, 1989).

Calculated home range of 20 *R. humulis* in Virginia, using five or more captures, averaged 952.4 m^2 (range, 248–2244 m^2). Mean size of home range in males (905.1 m^2) and females (1,094.5 m^2) were not significantly different (Cawthorn and Rose, 1989). The average greatest distance between four or more captures during May-October was 85.5 m, but for the November-April period was 46.2 m (Dunaway, 1968). In a short-term study using radioactive tagging, Kaye (1961*b*) found a very complex picture of spatial relationships. *R. humulis* is apparently not territorial (Cawthorn and Rose, 1989; Dunaway, 1968; Kaye, 1961*b*).

Nests in the wild are constructed of finely shredded grasses and are globular in shape (Kaye, 1961*b*). Nests vary in diameter from 11 cm in winter to 5 cm in summer. Nests are typically only 50% as high as wide. Nests may be placed in the center of clumps of grass, but more commonly they are on the ground, hidden at the base of a grass clump, or in a shallow depression apparently dug by the mice. Kaye (1961*b*) also found a ground nest built in the center of an abandoned *Sigmodon hispidus* nest. Nests are usually on the periphery of a home range with as many as four nests being used during a week. Twelve nests of *R. humulis* examined by Kaye contained a single small cavity large enough for only a single

mouse. However, in nests of man-made structures (traps, boxes, or cans) in winter, as many as six animals (with variable sex ratios) huddle together, apparently to conserve heat (Dunaway, 1968). There is no evidence that *R. humulis* produces its own runways; in most regions it probably uses the runways of *Sigmodon hispidus* (Hamilton and Whitaker, 1979).

Reithrodontomys humulis is found in association with several species of small mammals (Briese and Smith, 1974; Chandler, 1984; Gottschang, 1965; Shadowen, 1956; Stankavich 1984; Whiting and Fleet, 1987). In southwestern Ohio, Gottschang (1965) recorded the following small mammal associates (in descending order of abundance): *Microtus ochrogaster, M. pennsylvanicus, Peromyscus maniculatus, Blarina brevicauda, P. leucopus, Cryptotis parva, Reithrodontomys humulis, Synaptomys cooperi, Sorex cinereus, Pitymys (Microtus) pinetorum*, and *Mus musculus*. In eastern Texas, Whiting and Fleet (1987) recorded the following small mammal associates: *Sigmodon hispidus, Neotoma floridanus, Peromyscus gossypinus, Reithrodontomys fulvescens, Peromyscus (Ochrotomys) nuttalli, Oryzomys palustris, Blarina brevicauda, Pitymys (Microtus) pinetorum, R. humulis*, and *Mus musculus*. In neither study did *R. humulis* contribute significantly to small mammal abundance.

Records of predation on *R. humulis* are rare, but this species undoubtedly contributes to the diets of several mammalian, avian, and reptilian predators. Presence of one or more *R. humulis* skulls in barn owl (*Tyto alba*) pellets has been reported (Bailey, 1923; Handley, 1949; Smith et al., 1974; Steward et al., 1989; Wolfe and Rogers, 1969). Killing and at least partial consumption of *R. humulis* by other rodent species (*Microtus pinetorum, Peromyscus leucopus*, and *Ochrotomys nuttalli*) when caught in the same trap was reported by Dunaway (1968).

One ectoparasite, a mite (*Cheyletus eruditus*), has been reported for *R. humulis* (Lowery, 1974). An internal parasite, the liver trematode, *Zonorchis komareki* (Family Dicrocoeliidae), was reported in the bile ducts of one mouse of 12 collected (McKeever, 1971). Despite additional studies, no other parasites have been recorded (Dunaway et al., 1967; Zimmerman et al., 1987). Reasons for the relative absence of parasites include several host characteristics, such as typically small population sizes and no colonial tendencies. Small size may reduce location by ectoparasites, and a primarily granivorous diet makes it unlikely that they obtain internal parasites from contaminated animal parts.

Mean estimates of lifespan in the field for *R. humulis* in Virginia were 10.1 weeks for males and 8.7 weeks for females (overall mean of 9.5 weeks—Cawthorn and Rose, 1989). However, several mice in the study area lived >20 weeks with one mouse surviving >10 months. Average lifespan of *R. humulis* in captivity is considerably longer, up to 818 days (n = 69—Dunaway, 1968). Care and rearing of *R. humulis* in captivity is discussed by Layne (1959).

Trapping of *R. humulis* is difficult. Those techniques which mechanically exclude larger species and use traps designed to be tripped by animals in the weight range of *R. humulis* are preferred. Traps based on the Fitch (1950) design have been most successful. Pitfall traps are up to five times more productive than live traps (Briese and Smith, 1974). *R. humulis* avoids traps scented by *Microtus pinetorum* (Adams and Gettinger, 1988); thus, trapping success may be affected by previous use of the trap.

BEHAVIOR. Adult behavior develops over the first two weeks of life (Layne, 1959). At 4 days of age the semiprehensile tail responds to a slight touch by bending towards the stimulus. At 1 week of age, the front limbs are more coordinated than the hind ones. When disturbed in the nest, a defense reaction that is sometimes seen in adults, that of lying on the back and kicking violently, appears. At 10 days of age, following opening of eyes and ears, young are more active and no longer drag their venter when walking. At 12 days, young can sit erect on their hind legs and wash in an adult manner, starting with the snout, followed by the pinnae, flanks, and lastly grooming the tail from base to tip. At 2 weeks of age, young *R. humulis* behave like miniature adults. Frequent handling does not seem to alter the nervous and jumpy temperament of *R. humulis*. Excited responses of adults, observed in the laboratory, can be placed into two categories: a noticeable increase in external respiration, and a whipping movement of a stiffened tail to produce a rattling sound when the tail is in contact with the cage or nest box (Kaye, 1961*a*). Few data are available on mating behavior.

In general, young and adults are very tolerant of other individuals (Layne, 1959). All animals in a cage or aquarium share a common nest and only shortly before and after parturition are nest mates excluded by the pregnant or postpartum female. Fighting has only been observed in a cage housing several adult males, and they appeared to be the only participants (Layne, 1959). Parents killing, and at least partially consuming, their young has been reported (Dunaway, 1968; Kaye, 1961*a*). In addition, Kaye (1961*a*) reported that two 30-day-old females were consumed by two litter mates.

Evidence of sociality in *R. humulis* has also been observed in the field. In Virginia 8% of *R. humulis* captures were multiple captures, although none occurred during summer months (Chandler, 1984). Multiple captures have been reported elsewhere (Briese and Smith, 1974; Dunaway, 1968; Taulman et al., 1994); however, unlike Chandler's (1984) results, most or all of these multiple captures were male-female pairs. Winter nests may contain up to six animals, with uneven sex ratios (Dunaway, 1968). Although multiple nesting and multiple captures are evidence of sociality, *R. humulis* may be less sociable than *R. megalotis* (Chandler, 1984).

Females defend young until they have started to eat solid food (Kaye, 1961*a*). The female scoops the young under her body and commences to bite and push away the intruding object. Retrieval of young outside the nest by the female consists of grasping the young's body in her mouth at any convenient spot, including a foot, and returning the animal to the nest. Thorough cleaning of the young typically follows retrieval. Only one retrieval and cleaning of young by an adult male has been reported (Layne, 1959).

In captivity, toilets are confined to the corners of the cages and only rarely are wastes found in the nest box or food tray (Kaye, 1961*a*). In the field, no food caches were found in nests located by Kaye (1961*b*), but limited food caching sometimes occurs, with caches consisting of grass and sedge seeds (Hamilton and Whitaker, 1979). As with most cricetid rodents, *R. humulis* is primarily nocturnal, but diurnal activity apparently is common in the winter (Dunaway, 1968; Kaye, 1961*b*).

GENETICS. The diploid number of chromosomes in *R. h. merriami* is 50 and the fundamental number is 49 (Bradley et al., 1988; Engstrom et al., 1981). The karyotype has 47 acrocentric autosomes that are small to medium-sized, one metacentric autosome that is medium-sized, a small metacentric Y chromosome, and a large subtelocentric X chromosome (Bradley et al., 1988). Conflicting chromosomal numbers have been reported: *R. h. merriami*, 2n = 51, FN = 78 (Robbins and Baker, 1980); *R. h. humulis*, 2n = 51, FN = 78 (Robbins and Baker, 1980); *R. h. humulis*, 2n = 51, FN = 60 (Carleton and Myers, 1979). This represents considerably greater karyotypic variation than is normally seen in a single species (Baker et al., 1987).

Use of G- and C-banding studies indicates that a minimum of 15 events (nine heterochromatic additions and six pericentric inversions) were necessary to derive the *R. humulis* karyotype from a more primitive karyotype such as that of *R. fulvescens* (Robbins and Baker, 1980). Complete or partial homologies exist between these two species for at least the first 11 pairs of chromosomes. Starch-gel electrophoresis was used to examine 20 isozymes in homogenates of heart, kidney, and liver tissues in six species of *Reithrodontomys* (Arnold et al., 1983). *R. humulis* showed the greatest variety of isozymes of the six species, including allozymic variants. Species variability is primarily attributable to intraspecific differentiation between *R. h. humulis* and *R. h. merriami* specimens. Electrophoretic data, along with the considerable karyotypic variation, suggest some reproductive isolation between subspecies.

REMARKS. The word *Reithrodontomys* is derived from three Greek words that mean groove-toothed mouse (*rheithron*, groove; *odous*, tooth; *mys*, mouse–Lowery, 1974). The specific name *humulis* is thought by Lowery (1974) to have been a spelling error by Audubon and Bachman (1841), and he suggests that the authors intended *humilis* to be the specific name. The first spelling denotes a plant called hops, the second spelling denotes something small. The authors referred to this animal as the "little harvest mouse," and then later in their book *Quadrupeds of North America* (1851-1854) spelled the specific name *humilis*.

Reithrodontomys humulis was the first member of its genus recognized, but it was incorrectly placed in the genus *Mus* by Au-

dubon and Bachman (1841). Although it has been known the longest and has a wide distribution, difficulties in trapping have prevented this species from being one of the better understood of the five species of *Reithrodontomys* occurring in the United States. I thank F. Thomas in the Interlibrary Loan Department at Northwestern State University, Eugene P. Watson Library for assistance in obtaining articles from other institutions, and M. Romero for help in preparing Fig. 3.

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